This is to certify that the
dissertation entitled

STATUS AND DISTRIBUTION OF FROGS AND TOADS IN SOUTHERN MICHIGAN: POPULATION TRENDS AND THE INFLUENCE OF HABITAT AND LANDSCAPE CHARACTERISTICS

presented by

KRISTEN S. GENET

has been accepted towards fulfillment
of the requirements for the

Ph.D degree in Zoology and Ecology, Evolutionary Biology and Behavior

Thomas M. Burton
Major Professor's Signature

August 23, 2004
Date

PLACE IN RETURN BOX to remove this checkout from your record.
TO AVOID FINES return on or before date due.
MAY BE RECALLED with earlier due date if requested.

DATE DUE	DATE DUE	DATE DUE
FEB 0 2006 5 12 0 3 9 9		
JUL 1 9 2007		
0 5 0 [illegible] 0 7		

STATUS AND DISTRIBUTION OF FROGS AND TOADS IN SOUTHERN MICHIGAN: POPULATION TRENDS AND THE INFLUENCE OF HABITAT AND LANDSCAPE CHARACTERISTICS

By

Kristen S. Genet

A DISSERTATION

Submitted to
Michigan State University
in partial fulfillment of the requirements
for the degree of

DOCTOR OF PHILOSOPHY

Department of Zoology

2004

ABSTRACT

STATUS AND DISTRIBUTION OF FROGS AND TOADS IN SOUTHERN MICHIGAN: POPULATION TRENDS AND THE INFLUENCE OF HABITAT AND LANDSCAPE CHARACTERISTICS

By

Kristen S. Genet

Declining amphibian populations in many disturbed and pristine habitats worldwide have been the source of great concern and research in amphibian biology and conservation. Research conducted at multiple spatial scales, life history stages, and over long periods of time (at least 10-15 years) needs to be conducted and synthesized to fully understand amphibian population dynamics so that effective management and conservation strategies can be formulated. I investigated some of these issues for 12 species of anurans native to southern Michigan. My objectives were to: (1) assess the occurrence, distribution, and status of each species using multiple methods to analyze data collected by volunteers in the Michigan Frog and Toad Survey (MFTS) from 1996 to 2002, (2) evaluate the quality and consistency of data collected by observers in the MFTS and assess implications for population trends analyses of volunteer-collected data, (3) investigate relationships between anuran abundance and distribution and land cover adjacent to wetland breeding sites and within potential dispersal distances using GIS analyses, and (4) determine the potential influences of habitat characteristics on growth, development, and survival of larval *Pseudacris crucifer* in natural wetlands. Populations of all Michigan anurans were variable over the seven-year duration of the study, but no major declines were detected. Seven species did show statistically significant trends in site occupancy or abundance (assessed by calling intensity of breeding males), but trends were not consistent in direction across species and were small in magnitude. These trends need to be evaluated over longer time periods to determine whether they represent significant long-term population trends or short-term changes related to climatic variation. Volunteer observers in the MFTS were reliable more than 80 percent of the time in identifying all species of frogs and toads combined from their species-specific mating calls, but there was considerable variability in assessing abundance (i.e., assigning of categorical call index values to calling males). Volunteer background or prior experience in wildlife biology had little influence on data quality. Given variability among volunteers (and years) in abundance estimation, the poor understanding of empirical relationships between call index values and true breeding population size, the most robust analyses of MFTS data are those that use presence/absence (i.e., detection/non-detection) data. Food availability, hydroperiod, canopy cover, and predators affected *P. crucifer* tadpole development, survival and growth in wetlands in southwestern Michigan. Growth, development, and survival were greatest at sites with intermediate hydroperiods, partial canopy cover, and few (if any) fish predators. Land cover types influenced presence and abundance of anurans at wetland breeding sites. Land cover types indicating habitat alteration or loss (e.g., roads, urban) negatively influenced presence and/or abundance of anurans while land cover types representing important foraging and breeding habitats (e.g., open land, wetlands) represented positive influences. Species richness was not correlated with either the amount of adjacent forest cover or the amount of forest cover in the landscape within 1000 meters of breeding sites. Associations between anuran presence and abundance at breeding sites and land cover adjacent to and within 1000 meters of the breeding sites combined with data from population trends analyses provide valuable insights that can be used to identify critical habitats for management and conservation of these species.

TABLE OF CONTENTS

CHAPTER FOUR
The Influence of Local Habitat Characteristics on the Growth, Development, and Survival of Spring Peeper (*Pseudacris crucifer*) Tadpoles in Southwestern Michigan

LIST OF TABLES

LIST OF FIGURES

Status and distribution of frogs and toads in southern Michigan: Population trends and the influence of habitat and landscape characteristics

Introduction

The issue of declining amphibian populations in many locations worldwide has been the source of both great concern and research over the past two decades. While declines in some areas have been attributed to relatively unambiguous causes (e.g., Johnson 1992, Hayes and Jennings 1986), the situation remains enigmatic in other areas where habitats remain intact and no obvious sources of disturbance to natural population dynamics have been identified (e.g., Richards et al. 1993, Lips 1998). Some issues concerning anuran amphibians in the midwestern United States have been addressed (e.g., Lannoo 1998), but the factors affecting population dynamics of many species in this region remain poorly understood.

The hypothesized causes for widespread amphibian declines include habitat modification, chemical contamination (including acidification), predator introductions, global climate change, ultraviolet radiation, disease, parasitic infections, or synergistic interactions among multiple factors (e.g., Blaustein et al. 1994a, Sarkar 1996, Green 1997b, Alford and Richards 1999). The best documented amphibian declines have been attributed to habitat modification. Habitat loss is unambiguously related to reduced amphibian abundance and diversity (Johnson 1992, Hecnar and M'Closkey 1996, Hecnar 1997). Alteration of breeding, foraging, and/or overwintering habitats also has drastically impacted amphibian populations (e.g., Welsh 1990, Delis et al. 1996). Environmental contaminants and acidification negatively affect amphibian populations. The effects of acidification have been well documented (e.g. Freda and Dunson 1986, Freda et al. 1991), and environmental contaminants also reduce growth, development, and survival of anurans (Power et al. 1989). However, the long-term effects of routinely applied non-point source environmental contaminants (e.g., pesticides) have not yet been determined (Bishop 1992). Predation plays a very important role in the distribution and abundance of amphibians at all life history stages (e.g., Alford 1999). Widespread introductions of predatory game fish into formerly fish-free habitats, as well as the introduction of bullfrogs outside their native range, have led to dramatic reductions in amphibian diversity at some sites (e.g., Bradford 1989, Lannoo et al. 1994, Fisher and Shaffer 1996). Ultraviolet radiation reduces survival of eggs and tadpoles, and has been implicated as a causal factor in high altitude regions with species that breed in shallow, clear water (e.g., Blaustein et al. 1994b, Blaustein et al. 1997, Licht and Grant 1997). Global climate change has the potential to dramatically impact amphibian populations either through shifts in phenology and/or breeding site use (Beebee 1995, Gibbs and Breisch 2001) or interacting with other factors such as disease or a pulse of contaminants (Pounds and Crump 1994).

Anuran distribution is a function of the morphological and hydrological characteristics of wetlands, habitat heterogeneity within wetlands, community interactions, and habitat/breeding site availability and suitability for adults (Smith 1983, Wilbur 1984). Characteristics of both the local habitat and landscape setting affect the distribution and abundance of anurans. Landscape patterns are an important influence on adult distributions while larval communities and juvenile recruitment respond more to local habitat characteristics (Bunnell and Zampella 1999). The primary factors structuring tadpole communities are hydrology, predation, and competition (Smith 1983, Berven 1990, Skelly 1997). Adult communities are structured through a complex suite of interacting factors including wetland size, isolation, hydrology, substrate characteristics, and the distribution of suitable aquatic and terrestrial habitats throughout their life history (Wyman 1988, Laan and Verboom 1990, Skelly et al. 1999). Anuran communities are influenced by habitat factors that determine success and fitness at the population level and landscape factors that determine which habitats are suitable (Lehtinen et al. 1999).

Evaluating responses of frogs and toads to habitat and landscape characteristics during adult and larval stages of their life history should lead to a greater understanding of relationships between local habitats and landscape variables for current populations and result in improvements in the ability to project effects of climate and landscape changes on future populations. As a result, we will be better able to identify, manage, conserve, and preserve critically important components of natural ecosystems. The objective of this study was to provide such data for Michigan frog and toad populations. This study included the use of large-scale amphibian monitoring data from the statewide Michigan DNR Frog and Toad Survey, implementation of geographic information systems (GIS) as a tool to investigate patterns of amphibian distribution relative to potential influential factors (e.g., climate, land cover), and evaluation of larval amphibian communities in 10 wetlands in southwestern Michigan.

The specific objectives of this study were to:

(1) Assess the occurrence, abundance, distribution and projected status of each of Michigan's species of anurans using data collected by volunteers for the Michigan

Frog and Toad Survey (MFTS). This objective was addressed in Chapter One by evaluating species' distribution and site occupancy from1996 to 2002, calculating population trends for each species, and comparing results using the multiple analytical methods that have been used in other monitoring programs (e.g., Mossman et al. 1998).

(2) Evaluate the quality and consistency of data collected by multiple volunteer observers for the MFTS. This objective was addressed in Chapter Two using data collected from a mail survey of active MFTS volunteers to evaluate how volunteer background and experience influenced anuran identification and abundance estimation. Data quality related to observer differences should be included as covariates in population level analyses if possible (Sauer et al. 1994, Kendall et al. 1996).

(3) Investigate relationships between anuran abundance and distribution and land cover adjacent to and within their potential dispersal distance surrounding wetland breeding sites using GIS analyses. This objective was addressed in Chapter Three. Hypotheses tested were that amphibians would be (1) positively associated with land cover types representing necessary habitat during some portion of their life cycle (e.g., forest, wetlands) and (2) negatively associated with land cover types representing habitat loss or alteration (e.g., urban, roads).

(4) Determine potential influences of habitat characteristics on growth, development and survival of larval Spring Peepers (*Pseudacris crucifer)* in natural wetlands. Conditions in the aquatic larval habitats can have a profound influence on tadpole

performance and ultimate metamorphosis (Wilbur and Collins 1973, Alford 1999). This objective was addressed in Chapter Four.

Chapter One

Short-term population trends and status of frogs and toads in southern Michigan (1996-2002)

Abstract

The Michigan Frog and Toad Survey (MFTS), a volunteer-based amphibian monitoring program, was established in 1996. Volunteers have since collected data annually on abundance and distribution of Michigan's 13 species of anurans. The MFTS used protocols similar to other states and the North American Amphibian Monitoring Program, so these results are comparable to other regional surveys. Volunteers surveyed routes, each consisting of ten sites, after dusk on three dates each spring and recorded the identity and index of calling intensity of breeding males. Population trends and status of each species in southern Michigan were assessed using the MFTS data from 1996-2002. Trend analyses indicated that populations of all species were highly variable through time. Significant declines were not detected in Michigan. However, there were some significant but slight trends detected. *Rana catesbeiana* increased in site occupancy, while *Rana palustris* decreased. Mean annual call index increased over the study period for *Rana sylvatica, Pseudacris crucifer, H. versicolor/chrysoscelis,* and *Rana clamitans,* while *Bufo americanus* decreased. *Rana catesbeiana* also increased in route frequency and abundance, while *Hyla versicolor/chrysoscelis* decreased. *Rana palustris* and *Acris crepitans blanchardi* were too rare to be evaluated with statistical methods. This study provides a six-year baseline record that can be used to track future anuran population trends and identify declines in time to implement appropriate conservation measures.

Introduction

Since the early 1990's, researchers have recognized that amphibian populations worldwide have been suffering seemingly inexplicable declines (e.g., Blaustein and Wake 1990, Pechmann et al. 1991, Alford and Richards 1999). This is disturbing as amphibians play important roles in many ecosystems. Many of their characteristics render them good biological indicators of habitat quality, such as complex life cycles, trophic relationships, permeable skin, use of both terrestrial and aquatic habitats, and sensitivity to water chemistry during early life history stages (Stebbins and Cohen 1995, Bowers et al. 1998, U.S. EPA 2002). The hypothesized causes for widespread declines include habitat modification, environmental contamination (including acidification), predator introduction, global climate change, ultraviolet radiation, disease, parasitic infections or synergistic interactions among multiple factors (e.g., Blaustein et al. 1994a, Sarkar 1996, Green 1997b, Alford and Richards 1999). The primary obstacle for evaluating amphibian declines is separating effects due to anthropogenic influences from natural population fluctuations (Pechmann and Wilbur 1994, Travis 1994). To do this, long-term data from extensive areas are needed (Blaustein et al. 1994a). Regional amphibian monitoring programs can contribute such information. The values of data from long-term monitoring programs include identification of distributional changes and the ability to distinguish regional and long-term trends from local or short-term events not representative of population level phenomena.

Surveys of calling anurans (hereafter call surveys) at wetland breeding sites are being used for amphibian monitoring in many states and Canadian provinces (e.g., Huff 1991, Bishop et al. 1997, Lepage et al. 1997, Mossman et al. 1998). These surveys have potential to provide valuable information about population size and status (Zimmerman 1994, Shirose et al. 1997, Driscoll 1998). Call surveys are an efficient and effective method of surveying anurans over large geographical regions (Scott and Woodward 1994), and have successfully allowed collection of data on presence and abundance of frogs and toads in many areas. Call survey protocols are easy for volunteers to learn and provide the additional benefit of promoting education about wetland ecosystems and amphibian conservation.

The Wisconsin Department of Natural Resources (WDNR) was the pioneer in developing protocols for call surveys at breeding sites. The Wisconsin Frog and Toad Survey (WFTS), initiated in 1981, was the model for many state and national amphibian monitoring programs (Mossman and Hine 1984, Mossman et al. 1998, Weir and Mossman, in press). Developed in response to known or suspected declines in some anuran species, the WFTS was based on the successful North American Breeding Bird Survey (BBS, Robbins et al 1986, Peterjohn et al 1994). The original WFTS protocols were subsequently modified and extended to the national level for the North American Amphibian Monitoring Program (NAAMP) that was established in 1994. NAAMP developed a unified protocol for volunteer-based call surveys that has been implemented in 24 states so far (Weir and Mossman, in press).

In 1996, the Michigan Department of Natural Resources (MDNR) established an annual statewide frog and toad survey that used a network of volunteers to monitor breeding anuran populations (Sargent 2000). The Michigan Frog and Toad Survey (MFTS) protocol was based on the successful WFTS. Michigan also contributes data from several survey routes to NAAMP. The goals of the MFTS are fourfold: (1)

determine abundance and distribution of anurans in Michigan, (2) identify areas of concern where more intensive research efforts should be allocated, (3) educate local citizens and raise awareness of anurans and wetlands ecosystems, and (4) promote a positive relationship between citizens and the MDNR as a result of this volunteer-based program (Sargent 2000).

Call surveys contribute useful information for amphibian monitoring programs provided several assumptions are met and/or acknowledged (Link and Sauer 1997). These assumptions include: (1) call index values accurately represent numbers of breeding males, (2) breeding (calling) males accurately reflect population size of that species (i.e., sex ratio approximately equal or proportion of males and females in the population is stable), (3) proportion of calling males heard and estimated remains constant over time, (4) observers are reliable, and (5) patterns of change in call index values generally track patterns of change in actual population sizes. Shirose et al. (1997) demonstrated that call counts of some species of anurans are linearly related to chorus size. Thus, methods that base call index values on estimates of numbers of breeding males should provide meaningful approximations of abundance. Quality of MFTS observers was addressed in Genet and Sargent (2003, see also Chapter Two).

Michigan is home to 13 species of frogs and toads (see Harding 1997, Conant and Collins 1998). These species breed according to a predictable phenology beginning in early spring and extending into summer (Figure 1.1). One species, Blanchard's cricket frog (*Acris crepitans blanchardi*) is a species of special concern in Michigan, and has been suffering recent distributional and population declines (Lee 1998, Lehtinen 2001). Other than anecdotal reports, not much is known about the status and population trends of other species. Data from the MFTS are intended to identify species or areas of concern in need of further research and/or conservation efforts.

The MFTS currently has data for hundreds of survey routes (approximately 350 routes statewide) collected from 1996 through 2002. I investigated patterns of abundance and distribution for Michigan's anurans in the area where survey routes were most heavily clustered, the southern lower peninsula. Specifically, my objectives were to use the MFTS data over the time period of 1996-2002 to assess: (1) distribution of each species and changes in site occupancy over time, (2) population trends for each species, (3) effectiveness of multiple analytical techniques implemented by other amphibian monitoring programs (e.g., Mossman et al. 1998), and (4) effectiveness and contributions of the MFTS to long-term amphibian monitoring programs.

Materials and Methods

Michigan Frog and Toad Survey

The Natural Heritage Program in the Wildlife Division of MDNR established survey routes and recruited volunteers for the MFTS beginning prior to the anuran breeding season in 1996. Data are collected annually by volunteers; there are currently seven years of data available for approximately 350 frog and toad survey routes throughout Michigan. The routes are most heavily clustered in southern Michigan (Figure 1.2). Detailed protocols for the MFTS (Sargent 2000) are summarized below. Volunteers establish routes by submitting a map and descriptions of a series of 12 potential survey sites identified outside the anuran breeding season (i.e., without consideration of habitat suitability or frog presence). Volunteers classify sites along survey routes into one of six wetland type categories: (1) vernal pond, (2) wet meadow, (3) bog or fen, (4) marsh, (5) wooded swamp, (6) pond (Table 1.1, Sargent 2000). The state coordinator evaluates route location and suitability of each site along the route and mails data sheets and instructions to volunteers. Each accepted route consists of 10 wetland sites separated by at least 400 m, so that origin of calls can be unambiguously determined for each site.

The volunteers survey routes three times each spring and record the identity of each species and an index of calling intensity. The three suggested survey periods are early spring, mid to late spring, and summer, when minimum air temperatures are approximately 7°, 13°, and 18° C, respectively. Michigan anurans breed according to a predictable phenology that is largely dependent on weather conditions (Figure 1.1), and the three survey periods encompass significant breeding effort by each species. Volunteers conduct surveys beginning one-half hour after sunset and finishing before midnight under favorable conditions of appropriate temperatures and little or no wind. They wait at each site for 3-5 minutes before recording data to allow frogs to acclimate to their presence, and then listen for an additional 5 minutes to identify all calls and assess their intensity. Intensity of calling males is rated 0 through 3, with 0 = no individuals calling, 1 = few individuals with non-overlapping calls (1-5 individuals), 2 = distinguishable individual calls that overlap (6-12 individuals), and 3 = full chorus with indistinguishable individual calls (>13 individuals).

After the three survey runs have been completed, volunteers return data sheets to the MFTS state coordinator by 15 August each year. Verification in the form of recordings or photos is encouraged for rare species or reports from outside a species' documented range. Documentation is especially needed for *A. c. blanchardi*, and strongly recommended for *Hyla chrysoscelis* and *Rana palustris*.

Climatological Variables

Temperature and precipitation data were obtained from the state climatologist in the Geography Department at Michigan State University for 61 weather stations (contained within three climate divisions) distributed throughout southern Michigan (Figure 1.3). These data included daily average temperatures and precipitation for each station for 1996-2002. Daily data were condensed into monthly mean values corresponding to the anuran breeding season (February – July). Cumulative winter precipitation (rain and snowfall, Nov – Mar), which influences spring wetland inundation, was also determined for each climate station. These variables were statistically evaluated to determine differences among years, and examined for correlations with MFTS data using Spearman rank correlation analyses (Zar 1998). Correlations between climate variables and anuran abundance were determined for those months of spring wetland inundation and during the breeding season of each species (Figure 1.1). MFTS routes were matched to their nearest climate station using a GIS overlay of Figures 1.2 and 1.3. Route data were omitted from these analyses if no climate station data were available within the nearest county. Climate station data were omitted if more than 10% of days within a month (i.e., 3 days) were missing for the cumulative variables (monthly precipitation, total winter snowfall) or more than 25% of days (i.e., 8 days) were missing in a month for mean daily temperature.

Data Analyses

To be included in statistical analyses, each route needed to satisfy the following criteria: (1) all three survey runs were completed within a single year, and (2) routes were surveyed at appropriate times according to anuran breeding phenology. Data were condensed by determining the maximum calling index for each species for each site (i.e., merged data from all three survey runs for each year), and combining the two gray treefrog species (*Hyla versicolor* and *H. chrysocelis*). The calls of these two morphologically identical species are difficult to distinguish, and temperature can affect the pulse rate and duration of their calls, making them very difficult to identify in single species choruses (Harding 1997). Verification for *Hyla chrysoscelis* (in the form of recording or expert opinion) became a requirement for the MFTS in 1998, but prior to that the identities of the two treefrog species were not formally determined. Therefore, some records for *H. chrysoscelis* prior to 1998 may represent *H. versicolor* and vice versa. All data were graphically assessed for normality using box and normality plots prior to statistical analyses. Sample size was not equivalent in all wetland types or years (Table 1.2). As a result of this and some variables not satisfying assumptions of normality, both parametric and nonparametric analyses of variance were used in addition to linear regression.

Patterns of species richness in different wetland types in each year were evaluated with parametric and nonparametric analyses of variance (ANOVA and Kruskal-Wallis tests). Following these analyses, *post hoc* tests were utilized for pairwise comparisons; Bonferroni corrections were applied to all pairwise tests (Miller 1981). Trends of number of species in each wetland type over the seven years of this study were also evaluated with linear regression.

Several methods were utilized to analyze population trends. In analyses of WFTS data, Mossman et al. (1998) used techniques modified from trend analyses for BBS data (e.g., Geissler and Sauer 1990, Link and Sauer 1994). Four techniques were used to evaluate trends from the MFTS data: (1) site occupancy, (2) route frequency regression, (3) route index regression, and (4) adjusted route index regression. Site occupancy was determined by calculating the proportion of sites within each species' range (Harding 1997, Conant and Collins 1998) occupied in each year. The total number of sites where a species was present was summed and expressed as a proportion of the total number of sites surveyed each year. These annual proportions were arcsine transformed (Zar 1998) and regressed on year.

The other three route regression methods (frequency, index, and adjusted index) were similar to one another in that dependent variables were regressed on year, trends were determined for each route, and then averaged for all routes (Link and Sauer 1994, Mossman et al. 1998). Only routes where volunteers had submitted complete data for all 10 sites each year and that had been surveyed for at least three years were used in route regression analyses. Slopes for all route trends were statistically compared to zero with *t*-tests. The number of sites along each route where a species was present was summed for route frequency regression (range 0-10). The call index values were summed for all sites along a route for route index regression (range 0-30). For adjusted route index regression, a number was arbitrarily assigned to the call index that may better approximate the number of individuals present at each site (1 = 3 individuals, 2 = 9 individuals, 3 = 25 individuals). Mossman et al. (1998) arbitrarily assigned 3, 25, and 50 individuals for call index values 1, 2, and 3, respectively. However, given the instructions provided to volunteers, my approximations probably more accurately reflect relative abundance of calling males at a breeding site. The first two values represented midpoints of the range of numbers of individuals given as guidelines in survey protocols for call index values 1 and 2, and the third value represented the approximate number of individuals above which enumeration was not practical. These adjusted index values were then summed for all sites along a route (range 0 – 250). Data were log(x + 0.5) transformed before statistical analysis (Geissler and Sauer 1990, Zar 1998). Trends were determined and averaged across all routes for each species in southern Michigan and reported as slopes from regression analyses with associated 95% confidence intervals.

Data from routes that were surveyed by the same observers for all seven years were used for repeated measures analysis (von Ende 1993). This technique was used to evaluate changes in abundance and site occupancy along routes sampled repeatedly from 1996-2002. Only routes that were completely surveyed (i.e., all 10 sites each year, all three runs in each year, appropriate sampling dates, all seven years by same observers) were kept for repeated measures analyses, as the same variables calculated for route regressions were used (route frequency, route index, and adjusted route index). A total of 20 routes was included in the repeated measures analyses for all species except *Bufo fowleri,* for which 12 routes were within its range. Univariate repeated measures analysis was used, as it is generally considered more powerful than multivariate methods, and the degrees of freedom for the *F*-test were adjusted to accommodate for time as the within-subject factor (von Ende 1993). Statistical analyses were performed using SYSTAT (version 8.0; SPSS, Inc. 1998). Unless otherwise reported, $P < 0.05$ is considered statistically significant.

Results

During the first seven years of the MFTS, volunteers submitted data in at least one year, yielding a total of 269 routes in southern lower Michigan. With the exception of 1997, new routes were initiated each year, although the majority of routes was established in 1996 (Figure 1.4). Thirty-three percent of routes were surveyed for only one year, and > 60% of routes were surveyed for three or more years (Figure 1.5). Volunteers submitted data for all seven years for 61 routes (22.7% of total). Complete data for all 10 sites and three runs in each year for each route were submitted for 20 of those 61 routes.

Climatological Variables

Monthly means of air temperature and precipitation during each month of the anuran breeding season differed significantly among years during the time period 1996-2002 (Figure 1.6). April 1997 and 1999 were particularly dry, as were February 1997 and 2001 and March 1998 ($P < 0.001$). There was low precipitation in May 1998 and 1999, and in June 1998 and 2002. High precipitation occurred in May 2000 and 2001 and July 2000 ($P < 0.005$). The lower precipitation during May 1998 and 1999 ($F = 27.106$, $P < 0.001$, $df = 6$) corresponded to the peak breeding period for many Michigan anurans. During 1996, February and March temperatures were significantly lower than temperatures in these months in all other years ($P < 0.001$). Significantly higher low,

high, and daily mean temperatures occurred in February compared with February temperatures in all other years ($P < 0.001$).

Patterns of Species Richness

There were no consistent patterns of species richness among wetland types (Table 1.3), although vernal ponds had significantly fewer species than some other wetland types in 1998, 1999, and 2002 (Figure 1.7). The mean number of species in each wetland type also varied from 1996 through 2002 (Figure 1.8). Although there were significant differences in species richness within a given wetland type among years (Figure 1.8), no significant linear trend in mean number of species present over the seven years was detected for any wetland type (Table 1.4). All wetland types had the fewest species present during one or more years between 1998-2000. Linear trends did not fit the data well for any wetland type, explaining less than 1% of the variance in mean number of species over seven years (Table 1.4).

Site Occupancy and Calling Intensity

Bufo fowleri, Rana palustris, and *Acris crepitans blanchardi* were the least common species in southern Michigan, occurring at fewer than 4% of survey sites in their respective ranges (Table 1.5). Conversely, *Pseudacris crucifer* and *Hyla chrysoscelis/versicolor* were the most common species, occurring at more than 67% of sites (Table 1.5). *Rana sylvatica, Pseudacris triseriata, Bufo americanus,* and *Rana clamitans* were common, occurring at 30-60% of the survey sites (Table 1.5). *Rana pipiens* and *Rana catesbeiana* were less common, occurring at less than 20% of survey sites (Table 1.5). While most species fluctuated with no consistent trend in site occupancy over the seven year period, *R. palustris* declined significantly and *R. catesbeiana* increased significantly (Figure 1.9, Table 1.6).

Mean call index values varied among years for most species (Figure 1.9). *Pseudacris crucifer* and *H. chrysoscelis/versicolor* called at the highest abundance, with mean annual call index values > 2. Mean annual call index values of the remainder of species were either much more variable (e.g., *B. fowleri, A. c. blanchardi*) or less than 2. Although five species showed significant linear trends in call index values over time (*R. sylvatica, P. crucifer, B. americanus, H. versicolor/chrysoscelis,* and *R. clamitans*), these trends were not universal in direction nor did they explain much variability in the data (≤ 17%) (Table 1.7, Figure 1.9). *Bufo americanus* showed a trend of decreasing calling intensity, while the other four species increased in calling intensity over the same time period (Figure 1.9).

Site occupancy and calling intensity were significantly correlated with cumulative precipitation during the breeding season for *R. pipiens* (Table 1.8). *Acris crepitans blanchardi* call index values were marginally correlated with cumulative breeding season precipitation ($P < 0.10$, Table 1.8). The proportion of sites occupied by *Acris crepitans blanchardi* was also marginally correlated with cumulative winter precipitation ($P < 0.10$, Table 1.8). Neither site occupancy nor calling intensity was correlated with cumulative precipitation for any other species. Total annual snowfall (Nov – Mar) was significantly correlated with anuran route variables for *P. crucifer, H versicolor/chrysoscelis, A. c. blanchardi, R. clamitans,* and *R. catesbeiana* (Table 1.9). Significant correlations between cumulative monthly precipitation and all anuran abundance route variables were present for *R. palustris,* and *R. clamitans* in February, *R. sylvatica* in March, *R. clamitans* in April, and *R. clamitans* in July (Table 1.10). Significant correlations between mean monthly temperature and all anuran abundance route variables were present for *R. sylvatica* in February and March, *P. triseriata* in April, and *B. americanus* and *H. versicolor/chrysosclelis* in May (Table 1.11). Other species' individual route variables were also correlated with monthly precipitation or temperature, but were not consistent across all three route variables (Table 1.10-11).

Route Regression Analyses

Trends evaluated with the three route regression methods were similar, with most species showing no significant directional changes in presence and abundance over time (Tables 1.12 – 14). The two exceptions were *Hyla versicolor/chrysoscelis* and *Rana catesbeiana*. *Hyla versicolor/chrysoscelis* showed a slight but significant negative trend for all route regression dependent variables (Tables 1.12 – 14). *Rana catesbeiana* showed a slight but significant positive trend for all three route regression methods (Tables 1.12 – 14). The magnitude of the trend was small for both species, and the mean proportion of variance accounted for by time was also relatively small (< 40% and < 30% variance accounted for by all three route regression analyses for *H. versicolor/ chrysoscelis* and *R. catesbeiana*, respectively).

Repeated Measures Analyses

Rana palustris and *Acris crepitans blanchardi* were not reported in sufficient numbers along the 20 routes included in the repeated measures analyses, and were omitted from these analyses. Five species showed significant trends over time using route frequency, compared to three species for route index, and two species for the adjusted route index regression (Table 1.15). The two species with consistent significant trends for all three dependent variables were *Rana sylvatica* and *Rana clamitans* (Table 1.15). *Rana sylvatica* showed a significant 2nd order (quadratic) polynomial trend over the seven year period for route frequency, and 5th order (quintic) trend for route index and adjusted route index (Table 1.15); quadratic trends were marginally significant for this species for route index and route adjusted index ($P = 0.053$ and $P = 0.070$, respectively). *Rana clamitans* showed a significant 5th order trend for route frequency (linear trend marginally significant, $P = 0.083$); route index and adjusted route index showed linear trends (Table 1.15). Other species that showed significant trends over time included *Pseudacris crucifer*, *Hyla versicolor/chrysoscelis,* and *Rana catesbeiana* (Table 1.15). These three species were all characterized by either linear or quadratic trends for both route frequency and route index (Table 1.15).

Discussion

Volunteer-based anuran call surveys have the potential to provide long-term data on anuran distribution and abundance over broad geographical scales. Amphibian populations, however, can fluctuate dramatically under natural circumstances (i.e., Semlitsch et al. 1996), and the challenge is to identify trends in amphibian population dynamics that are potentially human-induced outside the range of natural variability (Pechmann et al. 1991, Pechmann and Wilbur 1994).

The mean number of species among different wetland types and within a single wetland type fluctuated over the duration of the study, but showed no consistent trends. Temperature and precipitation played roles in anuran presence and abundance at breeding sites, as has been well documented (e.g., Duellman and Trueb 1986, Stebbins and Cohen

1995). Total annual snowfall was most strongly correlated with *Pseudacris crucifer* occurrence and abundance, an early spring breeder. Snowfall was also significantly correlated with the three species that breed primarily in permanent ponds, *A. c. blanchardi, R. clamitans,* and *R. catesbeiana,* perhaps indicating the importance of seasonal recharge of these ponds via either meltwater or groundwater inputs. Most of the species showed significant correlations with temperature and/or precipitation during the months of peak breeding activity. Surprisingly, *R. sylvatica* occurrence and abundance was negatively correlated with both temperature and precipitation during its breeding season. This is an explosively breeding species that may be often overlooked in call surveys (Crouch and Paton 2002), and unless the spring thaw is abnormally delayed, volunteers may often miss their peak breeding effort before conducting the first survey run.

Species Accounts

Rana sylvatica is typically one of the first species to emerge and breed each spring, usually concurrently with or following the onset of *Pseudacris triseriata* and *P. crucifer* calling (Figure 1.1). The unpredictability of suitable weather conditions, combined with its explosive breeding strategy (Berven 1990, Harding 1997) and tendency to call only when air temperatures exceed 9°C (i.e., during warm afternoons, Crouch 1999), make this species a challenge for observers to sample adequately in night call survey monitoring programs. *Rana sylvatica* was only reported from 23-41% of sites surveyed over the seven years of the study period. This may reflect low detection rates rather than real trends in distribution. To account for relatively low detection rates and temporal variability in calling behavior, NAAMP suggested adding an additional sampling period to target this species (Weir and Mossman, in press). The MFTS recommends that volunteers either conduct the first sampling period in conjunction with *R. sylvatica* breeding activity or conduct an extra, separate sampling period during warm afternoons in early spring specifically to target this explosively breeding species (L. G. Sargent, pers. comm.).

Rana sylvatica has a broad distributional range that extends farther north than any other North American amphibian species, and is considered common in suitable habitat virtually throughout its range (Harding 1997, Conant and Collins 1998). In this study, *R. sylvatica* typically called at intermediate calling intensities (mean annual calling index varied between 1.5 – 2), and showed a significant linear trend of increasing calling intensity over the study period. Route regression analyses using all routes did not show significant trends for wood frog populations. Repeated measures analyses, however, indicated significant population trends over time, although the higher order polynomial trends were difficult to interpret. These analyses suggest that *R. sylvatica* populations are variable, but provide no evidence that there are population declines in Michigan. This species is considered to be common and under no declines in the Great Lakes region (Pentecost and Vogt 1976, Weller and Green 1997, Casper 1998, Moriarty 1998). The WFTS data indicated a significant trend of population increase for this species, which is at least partially due to observers improving their survey techniques over time (Mossman et al. 1998). The MFTS data are consistent with these patterns observed in the WFTS.

Pseudacris triseriata was heard calling in 49-54% of sites surveyed each year of the study period and appears to have a stable, if not slightly increasing, pattern of site occupancy. This species consistently called at intermediate calling intensities (mean annual call index between 1.5 – 2). Over the duration of the study period, *P. triseriata* populations fluctuated, but there was no indication of declines. The lower frequency and acoustical carrying capacity of this species' call make it difficult to detect at sites where it is calling in a mixed chorus with more boisterous species (i.e., *Pseudacris crucifer*, see Chapter Two). Compared to other species, Varhegyi et al. (1998) found that the call of *P. triseriata* attenuated the most rapidly with distance, perhaps affecting its detectability from roadside listening sites. *Pseudacris triseriata* also frequently calls during daylight hours (Harding 1997). If their calling activity is reduced at night, this species may also be missed more frequently with nighttime call surveys. Perhaps in addition to *R. sylvatica, P. triseriata* could also be targeted with an earlier survey run before sunset.

My results are congruent with results for populations of *P. triseriata* in nearby states. There have been no reports of declines on a statewide basis for any nearby state (Pentecost and Vogt 1976, Brodman and Kilmurry 1998, Casper 1998, Mierzwa 1998, Moriarty 1998). However, the WFTS suggested that *P. triseriata* may be declining in some regions (Mossman et al. 1998). Others have also noted population declines for this species, especially in areas where habitat has been lost or altered (Daigle 1997, Weller and Green 1997, Harding 1997). *Pseudacris triseriata* is highly dependent on open marshes as well as wooded swamps, and is strongly influenced by climatological variables that determine both the timing of breeding events and suitability of habitat (i.e., meltwater and spring rains that fill wetlands) (Harding 1997); therefore any changes to their habitat could be translated to population level impacts.

Pseudacris crucifer is the most widespread and abundant anuran in southern Michigan, occurring at 79-89% of all sites surveyed, and calling at or above a mean annual calling index of 2.5. Based on these data, there is no indication that this species is suffering any population declines in southern Michigan. Similarly, throughout its range, this species is widespread and abundant (Harding 1997, Weller and Green 1997). However, significant but small declines have been noted in Wisconsin for *P. crucifer* despite a frequency of occurrence greater than all other species (Mossman et al. 1998). *Pseudacris crucifer* populations are well suited to monitoring with call surveys because of their high detection rates and consistent calling behavior (Mossman et al. 1998, Crouch 1999).

Rana pipiens was found at 11-17% of survey sites over the study period. This species typically calls at lower intensities or in smaller choruses than some other species (mean annual call index 1 – 1.5). The relative rarity of this species and the paucity of records for full choruses in call surveys could be due to the low volume of its call (Bishop et al. 1997) and/or could reflect decreasing distribution and abundance. *Rana pipiens* was generally very abundant in the Great Lakes region until the 1960s (Pentecost and Vogt 1976), and populations have since declined in many areas (Hine et al. 1981, Vogt 1981, Moriarty 1998, Mossman et al. 1998). Although *R. pipiens* can be locally abundant in open marshes (e.g., Harding 1997, Mierzwa 1998), several factors have contributed to declines in distribution and abundance throughout its range including drainage and conversion of wetlands for agriculture or aquaculture, exposure to pesticides, collection for the biological supply trade and bait, and introduction of bullfrogs in the western parts of its range (Lannoo et al. 1994).

Rana palustris has many similarities to *R. pipiens*, including similar calls and timing of breeding events; however, these species do not typically breed in the same habitats. In southern Michigan, *R. palustris* is poorly detected in call surveys, occurring at 1-3% of survey sites. Its breeding call is low and subtle, and it was not frequently heard calling above a call index value of 1. The low level of site occupancy of *R. palustris* precluded evaluation of population trends over time with repeated measures analysis. *Rana palustris* is generally uncommon, perhaps as a result of its preference for cool, clear waters and intolerance to pollution (Harding 1997). The limited data for *R. palustris* make evaluation of population trends difficult, although it did show a significant decrease in site occupancy over the study period (Figure 1.9, Table 1.6). The MFTS data suggest that this species is either rare, undersampled and/or confused with the similar looking and sounding *R. pipiens* (Genet and Sargent, 2003; see Chapter Two), but is persisting in suitable wetlands.

Bufo fowleri reaches the edge of its range in Michigan and is limited to the western and southern parts of the lower peninsula (Harding 1997). This species is either very rare or not detected well by the MFTS, as it was present at only 1-4% of all sites within its range over the study period. Presence at survey sites and mean annual call index values fluctuated over the study period, but did not show significant trends. Although *B. fowleri* is at the edge of its range in the Great Lakes region, others have reported that it is relatively widespread and locally abundant (Harding 1997, Brodman and Kilmurry 1998). Detailed investigations of demographic and life history characteristics of this species have provided information on population status in certain regions (e.g., Breden 1988, Green 1997a). Green (1997a) found that age structure and sex ratio of this species are unstable in Ontario populations, and call surveys are not likely to accurately reflect population size if only chorusing males are sampled. Similar detailed studies in Michigan would be of value to monitoring and conservation of *B. fowleri*.

Bufo americanus is common in southern Michigan, occurring at 34-42% of sites during the study period. This species typically called at intermediate abundances (mean annual call index 1.5 – 2). The prolonged trill of *B. americanus* makes it difficult to compare its call index values to other species with shorter calls (e.g., *P. crucifer*, *Rana clamitans*). The mean annual call index of *B. americanus* declined significantly over the study period, although little variance was explained by this relationship. No other significant changes in abundance or distribution (i.e., frequency of detection) were detected over the past seven years. This species is generally common throughout the Great Lakes region, but has experienced local population declines in some regions (Harding 1997). A review of the status of *B. americanus* in nearby states indicated that populations are stable, common and widespread, and that populations survive in altered habitats and during drought years (Brodman and Kilmurry 1998, Hemesath 1998, Mierzwa 1998, Moriarty 1998, Mossman et al. 1998).

Hyla versicolor/chrysoscelis is one of the most abundant and frequently encountered anurans in southern Michigan, occurring at 68-80% sites and frequently calling in small to large choruses (mean annual call index >2). This species showed a significant increase in calling intensity over the past seven years, although this relationship accounted for little variance in the data. This species also showed significantly decreasing population trends in all three route regression methods, as well as a significant polynomial trend in the repeated measures analyses. Although their calling intensity increased slightly over the duration of the study, route regression analyses indicated negative trends for all three dependent variables. This may indicate that there are more individuals calling from fewer sites. Another potential problem is that the data represent two treefrog species. These two morphologically identical species have similar calls that are influenced by temperature and difficult to distinguish (Gerhardt et al. 1994, Bertram and Berrill 1997). In southern lower Michigan, *Hyla versicolor* is more common than *H. chrysoscelis* (Harding 1997). This is also the case in Wisconsin (Mossman et al. 1998). *Hyla versicolor* and *H. chrysoscelis* appear to have stable populations and are common, and widespread (Weller and Green 1997, Brodman and Kilmurry 1998, Mossman et al. 1998).

Acris crepitans blanchardi is classified as a species of special concern by MDNR. Many populations have vanished from historical locations, although some isolated sites appear to have healthy populations in southern Michigan (Lee 1998, Lehtinen 2001). In southern Michigan, *A. c. blanchardi* was very rare, occurring at 0.3-3.2% of sites, and calling at variable intensities over the past seven years. The low frequency of occurrence precluded evaluation of population trends with repeated measures analyses. Route regression analyses did not indicate any significant declines. This species suffered drastic declines in northern portions of its range during the late 1970s and 1980s, and many previously healthy populations are now either greatly reduced or extirpated in the Great Lakes region (Harding 1997, Hay 1998, Mierzwa 1998). This is the only anuran with protected status in Michigan. Additional studies at specific sites should be conducted periodically to assess population viability, as the MFTS is unlikely to document significant population trends (other than extirpations) as a result of low frequency of occurrence in wetlands throughout the region.

Rana clamitans is a common and widespread species in southern Michigan, consistently occurring at 54-68% of sites surveyed, but calling at relatively low intensities (mean annual call index < 1.5). Although route regression methods did not indicate a significant population trend, repeated measures analyses indicated significant trends, usually in an upward direction. Although *R. clamitans* usually called in small numbers, their short distinct calls make it unlikely that they will be heard in full choruses of indistinguishable individuals even though many individuals may be actively calling from a breeding pond. Harding (1997) reported that *R. clamitans* is one of the most conspicuous and abundant anurans in the Great Lakes region, and others have also noted its abundance and ubiquity (Weller and Green 1997, Brodman and Kilmurry 1998, Mierzwa 1998, Mossman et al. 1998). The high frequency of occurrence of this species, coupled with its consistent calling pattern, make it well suited to population monitoring using call surveys (Crouch 1999).

Rana catesbeiana is the largest and longest-lived anuran in North America (Conant and Collins 1998). This species is relatively uncommon in southern Michigan, occurring at 14-20% of survey sites and calling at low intensities (mean annual call index <1.5). Despite its relatively low frequency of occurrence, *R. catesbeiana* showed significant population trends including increasing site occupancy and increasing trends for all route regression analyses. This species is native to eastern North America, but has been widely introduced to western regions, often with drastic consequences for native amphibian populations (e.g., Hayes and Jennings 1986, Fisher and Shaffer 1996). Generally, *R. catesbeiana* is either widespread (e.g., Mierzwa 1998) or irregularly distributed (e.g., Mossman et al. 1998). No evidence of significant declines of this species within its native range has been reported. *Rana catesbeiana* requires permanent water bodies as breeding ponds, as tadpoles overwinter and typically do not metamorphose until their second or third summer (Harding 1997). Perhaps the increasing trends noted for this species in southern Michigan reflects a change in the distribution of permanent waters in the region (Dahl 2000); a landscape level analysis of habitat change over the past decade would contribute to understanding these patterns.

Analyzing Population Trends from Call Surveys

Protocols and data analysis methods for amphibian call surveys have largely been adapted from BBS methodology (e.g., Geissler and Sauer 1990, Mossman et al. 1998). Even though anuran call surveys have been widely implemented in the U.S.A. and Canada, few programs have accumulated data long enough for meaningful analyses of population trends. Shirose and Brooks (1997) suggested that populations should be monitored for a minimum of the generation time of the longest-lived species surveyed. In Michigan, the longest lived species is *R. catesbeiana,* which lives at least 7-8 years in the wild (Zug 2001); its lifespan is potentially much longer, based on captive animals (Staniszewski 1995, Harding 1997). Optimally, species should be monitored over multiple generation times since they typically show lags between environmental impact and population level response (Shirose and Brooks 1997). Wisconsin is the only state that has accumulated call survey data over long enough time intervals to allow rigorous analyses (Mossman et al. 1998). I used the methods of Mossman et al. (1998) to facilitate comparisons of population trends in Michigan with trends for Wisconsin.

Several methods to analyze population trends from count data could potentially be modified to accommodate call index data, such as route regression and rank trends analyses (Thomas and Martin 1996), but consensus on the most accurate or reliable method is lacking. Thomas and Martin (1996) found that three common methods for analyzing population trends in BBS data generally produced similar results, but the number of significant declines in bird populations differed depending on the method used. They suggested that additional research on population trends analysis methods was warranted, as the ability to detect significant population declines and prioritize species for conservation efforts depend strongly on the method used.

The route regression analyses used here and in Mossman et al. (1998) are based on standard route regression methods for BBS data (Geissler and Sauer 1990). They involved evaluating trends over time for each route and averaging those trends for each region of interest. Three dependent variables were calculated (route frequency, route index, and adjusted route index), representing presence/absence (i.e., detection/ nondetection) and abundance data. Using a number of techniques to evaluate population trends appears prudent, as results can be compared among methods and redundancies used to select the most appropriate and useful methods. When significant trends are detected by multiple methods, confidence in the results also increases. Mossman et al. (1998) found route frequency regression to be the most useful technique because it accounted for differences in sampling intensity among regions and allowed analyses of routes not run every year. In my analyses, the three route regression analyses produced similar results, as did analyses of the proportion of sites occupied over time. The direction of each species' trend was the same for all route regression methods, except for *Rana sylvatica*. However, the only significant trends noted were a slightly decreasing trend for *Hyla versicolor/chrysoscelis* and a slightly increasing trend for *R. catesbeiana*.

Call index values were difficult to interpret, since adjusted route index regression involved arbitrary approximation of number of breeding males in a chorus. The call characteristics of each species influence perceived abundance and assignment of call index categories. In effect, it takes fewer individuals with a prolonged call such as *Bufo americanus* to be perceived at higher call index values of 2 or 3 than a species with a shorter call such as *Rana clamitans*. Sargent (2000) provided a numerical guide for call index values in addition to the subjective determination of the degree of overlap and distinction of individual calls as a means of making assignment of index values more uniform among volunteers (see Methods section). Even so, the relationship between the calling index and actual numbers of breeding males needs to be evaluated for each species before call index data can be reliably used to track changes in abundance. Researchers and managers generally agree that detection/nondetection data are the most valuable contributions of call surveys at the current time (Bishop et al. 1997, Bonin et al. 1997, Green 1997a, Lepage et al. 1997, Mossman et al. 1998, Weir and Mossman, in press). Volunteers should continue to record call index values so that these data can be used to evaluate changes in abundance once empirical relationships are developed (Weir and Mossman, in press).

Repeated measures analyses of variance (i.e., von Ende 1993) are widely used and provide a statistically rigorous means to evaluate changes at sites repeatedly sampled over time. This method allows evaluation of polynomial trends. Polynomial trends such as those seen in this study for *R. sylvatica* and *R. clamitans* are difficult to interpret and may be of little use or biological significance. Lower order trends were marginally significant ($P < 0.10$) for these species. If such trends are biologically meaningful, results could still be useful in planning for conservation and management of these species and should be reported. Repeated measures analyses are most useful when all sites have been surveyed for long periods of time. MFTS volunteers join and/or drop out of the surveys, so the number of sites included only represent a very small fraction of the total that can be used in other population trends analysis techniques. In this study, data from only 20 routes could be used in repeated measures analysis (12 routes for *B. fowleri*). The low sample size limits the power to detect significant trends, and the trends detected by repeated measures but not by other procedures (i.e., route regression) could be an artifact of this low sample size.

I agree with the suggestion of Mossman et al. (1998) to continue evaluation of multiple analytical techniques to evaluate trends in anuran call survey data. The MFTS is still a relatively young monitoring program. Although it is currently in its eighth year and has achieved the duration recommended by Shirose and Brooks (1997), the value of data for the identification of population trends increases over longer time scales. Perhaps ten years is a more realistic minimum for meaningful population trends analyses. Call surveys provide valuable information, but the data must be analyzed and interpreted within the limitations of the survey methodology. These limitations include data reliability, interobserver variation, dependence on volunteers for long-term data, subjective selection of survey routes, and poor understanding of how call index values are related to actual population size.

Management and Conservation Implications

Prior to the establishment of the MFTS, reports of anuran status, abundance, and distribution in Michigan were largely anecdotal or unknown. Trend analyses of the first seven years of data on the abundance and distribution of 13 species of anurans indicated that populations of all species fluctuated between years, but no significant declines were detected in Michigan. However, slight but significant trends in site occupancy, annual call index values, frequency and abundance that emerged from statistical analyses for *Rana sylvatica, Rana palustris, Rana catesbeiana, Pseudacris crucifer, Bufo americanus, Hyla versicolor/chrysoscelis,* and *Rana clamitans* need to be monitored closely, and if they continue, should be evaluated to determine potential influential or causal factors. Several species were poorly detected by call surveys in southern Michigan, and these species warrant additional attention at specific sites to determine if populations are stable or declining.

Anurans are dependent on wetlands for breeding, and many species require wetlands for their entire life cycle. Unfortunately, wetlands are also among the most endangered ecosystems in the world. Wetland habitats in the midwestern United States have suffered losses in excess of 75% for areas dominated by agricultural, industrial, and urbanized activity (Detenbeck et al. 1999). The landscape of southern lower Michigan is characterized by agriculture and urban development, and this region has experienced the greatest loss of wetlands in the state since the 1800's (Comer 1996). Conservation of Michigan's anurans will require conservation of their wetland habitats. Most wetland losses occurred from the late 1800's and early 1900's (Comer 1996). Thus, current surveys document status in remaining wetlands and highlight the need to protect and manage these ecosystems.

The MFTS collects valuable information concerning abundance and distribution of native frogs and toads. The value of this dataset increases as annual data are accumulated, providing a long-term record of species presence and abundance. Given reports of widespread declines worldwide and for some species in the Great Lakes region, these data provide evidence that Michigan frog and toad populations are relatively stable at present and also provide a baseline for determining species status and protecting species from future losses. The results are a conservative estimate of species trends; given the relatively low resolution of calling index data and the fact that species undetected by call surveys may not necessarily be absent from a site. The MFTS should continue to monitor frogs and toads indefinitely, as the overall population trajectory needs to be distinguished from the short-term fluctuations.

Acknowledgements

Correspondence with J. R. Sauer, M. J. Mossman, and L. Bailey aided in data analyses and interpretation. T. M. Burton, S. K. Hamilton, D. J. Hall and J. H. Harding provided valuable comments on earlier drafts. Support for this research was provided by the Michigan Coastal Management Program of the Michigan Department of Environmental Quality, National Oceanic and Atmospheric Administration, U.S. Department of Commerce, Geological and Land Management Division of the Michigan Department of Environmental Quality with funding from the State and Tribal Wetland Development Program, Region V of the U.S. Environmental Protection Agency, Great Lakes Wetland Research Consortium of the Great Lakes Commission with funding from the Great Lakes National Program Office, and the U.S. Environmental Protection Agency.

Table 1.1

Wetland categories assigned by volunteers to MFTS survey sites. Descriptions of wetland types are from Sargent (2000).

Wetland Type	**Description**
Vernal Pond	Vernal ponds are small bodies of standing water that form in the spring from meltwater and are often dry by mid-summer or may even be dry before the end of the spring growing season. Many vernal ponds occur in depressions in agricultural areas, but may also be found in woodlots. Wetland vegetation may become established but are usually dominated by annuals.
Wet Meadow	Wet meadows usually look much like a fallow field except that they are dominated by water-loving grasses and sedges. They will contain nearly 100% vegetative cover with very little or no open water. Any surface water present is temporary or seasonal and only during the growing season in the spring. Wet meadows often form a transition zone between aquatic communities and uplands with soils that are often saturated and mucky.
Bog or Fen	Bogs are found on saturated, acid peat soils that are low in nutrients. They support low shrubs, herbs and a few tree species on a mat of sphagnum moss. Some bogs are totally overgrown and some consist of open water surrounded by floating vegetation. Acid-tolerant plants found in and around bogs include woody plants such as labrador tea, poison sumac, tamarack, and black spruce. Many species of orchids prefer bog habitats, as do insect-eating sundews and pitcher plants. Bogs are usually only found in the northern part of Michigan. Fens are similar to bogs except that the soils are more alkaline because they result from water passing through calcareous deposits. Fens have a higher plant diversity than bogs due to higher nutrient levels. Fens can be found in the southern part of Michigan.
Marsh	Marshes have standing water from less than an inch up to 3 feet deep. The amount of water can fluctuate seasonally or from year to year. They are dominated by soft-stemmed emergent plants such as cattails and rushes. Vegetative cover is usually around 50%. In Michigan, marshes can be found at the edge of some rivers and lakes, in lowlands and depressions, and in swales between sand dunes.
Wooded Swamp	Wooded swamps are aptly named because they are dominated by woody plants such as shrubs and/or trees. The soil is saturated throughout the growing season. Some may become dry during the summer months. In Michigan, trees and shrubs found in wooded swamps include red and silver maple, cedar, balsam, willow, alder, black ash, elm and dogwood. They often occur along streams or on floodplains, in flat uplands or shallow lake basins.
Pond	Ponds are open bodies of water that are less than 20 acres in size and that do not dry up during summer months. There is little emergent vegetation but some floating vegetation may occur around the edges.

Table 1.2

Number of sites of each wetland type for which volunteers submitted complete data to the MFTS. Wetland types and years not satisfying the assumptions of normality are indicated with an asterisk (*).

Wetland Type	1996	1997	1998	1999	2000	2001	2002
Vernal Pond	165	111	142	150	123	134	73
Wet Meadow	110	80	106	91	71	68	42
Bog or Fen	34	14*	25	26*	18	15*	10*
Marsh	457	280	384	385	293	275	135
Wooded Swamp	388	285	355	327	265	258	127
Pond	434	296	363	370	267	270	138
Total	1588	1066	1375	1349	1037	1020	525

Table 1.3

Summary of parametric ANOVAs and nonparametric Kruskal-Wallis tests evaluating differences in species richness among wetland types each year, 1996 – 2002. Sample sizes are listed in the bottom row of Table 1.2, and all tests had 6 degrees of freedom.

Year	ANOVA F ratio	ANOVA P value	K-W H	K-W P value
1996	1.763	0.103	11.455	0.075
1997	1.599	0.144	8.312	0.216
1998	2.888	0.008	14.705	0.023
1999	5.203	<0.001	32.836	<0.001
2000	1.896	0.079	12.107	0.060
2001	0.562	0.760	2.651	0.851
2002	2.711	0.013	15.704	0.015

Table 1.4

Results of simple linear regressions of the mean number of species present in each wetland type over the time period 1996-2002.

Wetland Type	**R^2**	**P value**
Vernal pond	0.001	0.446
Wet meadow	0.001	0.552
Bog/fen	0.003	0.520
Marsh	<0.001	0.783
Wooded swamp	0.002	0.073
Pond	<0.001	0.670

Table 1.5

Proportion of all sites surveyed by each species, 1996-2002. The total number of sites for each species includes only those sites within the species range. Sample size (i.e., number of sites where present) for each species is given in parentheses in each year column.

Species	**1996**	**1997**	**1998**	**1999**	**2000**	**2001**	**2002**
Bufo fowleri	0.031 (36)	0.029 (19)	0.029 (21)	0.012 (10)	0.035 (25)	0.021 (8)	0.018 (5)
Rana sylvatica	0.335 (564)	0.256 (289)	0.260 (381)	0.318 (457)	0.226 (248)	0.356 (384)	0.408 (226)
Pseudacris triseriata	0.486 (817)	0.505 (571)	0.489 (716)	0.485 (697)	0.488 (536)	0.524 (565)	0.538 (298)
Pseudacris crucifer	0.834 (1402)	0.851 (962)	0.822 (1203)	0.790 (1136)	0.799 (874)	0.871 (939)	0.892 (494)
Rana pipiens	0.170 (286)	0.138 (156)	0.156 (229)	0.146 (210)	0.113 (124)	0.126 (136)	0.152 (84)
Rana palustris	0.021 (35)	0.013 (15)	0.014 (20)	0.014 (20)	0.012 (13)	0.003 (3)	0.009 (5)
Bufo americanus	0.420 (706)	0.407 (460)	0.347 (508)	0.344 (494)	0.374 (411)	0.366 (395)	0.421 (233)
Hyla versicolor/ chrysocelis	0.752 (1265)	0.763 (863)	0.693 (1014)	0.707 (1017)	0.676 (742)	0.788 (849)	0.800 (443)
Acris crepitans blanchardi	0.023 (38)	0.032 (36)	0.026 (38)	0.006 (9)	0.003 (3)	0.013 (14)	0.018 (10)
Rana clamitans	0.573 (963)	0.637 (720)	0.617 (903)	0.577 (830)	0.542 (595)	0.662 (714)	0.675 (374)
Rana catesbeiana	0.141 (238)	0.154 (174)	0.152 (223)	0.163 (235)	0.173 (190)	0.158 (170)	0.202 (112)

Table 1.6

Results of simple linear regressions for proportion of sites within ranges occupied by each species during the period 1996 – 2002. N = 7 for each species, representing each year of the survey since 1996.

Species	r^2	*P* value
Bufo fowleri	0.204	0.309
Rana sylvatica	0.199	0.315
Pseudacris triseriata	0.497	0.077
Pseudacris crucifer	0.186	0.366
Rana pipiens	0.235	0.270
Rana palustris	0.592	0.043
Bufo americanus	0.014	0.802
Hyla versicolor/chrysoscelis	0.088	0.518
Acris crepitans blanchardi	0.236	0.269
Rana clamitans	0.200	0.314
Rana catesbeiana	0.691	0.021

Table 1.7

Results of simple linear regressions evaluating trends in mean call index values for each species during the period 1996-2002. N = 7 for each species, representing each year of the survey since 1996.

Species	r^2	*P* value
Bufo fowleri	0.10	0.277
Rana sylvatica	0.10	<0.001
Pseudacris triseriata	0.01	0.194
Pseudacris crucifer	0.01	0.010
Rana pipiens	0.01	0.359
Rana palustris	0.02	0.665
Bufo americanus	0.04	<0.001
Hyla versicolor/chrysocelis	0.01	0.002
Acris crepitans blanchardi	0.17	0.119
Rana clamitans	0.02	0.004
Rana catesbeiana	0.01	0.257

Table 1.8

Correlations between cumulative precipitation during anuran breeding season (Feb-Jul) or cumulative winter (Nov – Mar) precipitation (rain and snowfall) and either proportion of sites within range occupied or mean annual call index values (1996-2002). Values are Spearman rank correlation coefficients (r_s; *p < 0.05, **p < 0.01).

Species	**Cumulative Breeding Season Precip.**		**Cumulative Winter Season Precip.**	
	Prop. occupied	**Call index**	**Prop occupied**	**Call index**
Bufo fowleri	0.270	0.179	-0.306	-0.536
Rana sylvatica	-0.607	-0.143	0.036	0.321
Pseudacris triseriata	-0.286	-0.450	0.536	0.090
Pseudacris crucifer	-0.357	-0.536	0.429	0.071
Rana pipiens	-0.786*	-0.964**	0.071	0.214
Rana palustris	-0.180	-0.487	-0.162	0.252
Bufo americanus	-0.107	0.643	-0.107	-0.571
Hyla versicolor/chrysoscelis	-0.286	-0.107	0.393	-0.036
Acris crepitans blanchardi	-0.429	0.714†	0.750†	-0.536
Rana clamitans	-0.429	-0.500	0.679	0.643
Rana catesbeiana	0.286	-0.214	-0.286	0.643

†P < 0.10

Table 1.9

Correlations between annual total snowfall prior to the anuran breeding season (Nov – Mar) and each species' route variables. Values are Spearman rank correlation coefficients (r_s; *p<0.05, **p<0.01). Sample size for each pairwise comparison is listed in parentheses following the species name.

Species	**Route Frequency**	**Route Index**	**Adj. Route Index**
Bufo fowleri (236)	0.090	0.092	0.092
Rana sylvatica (459)	0.025	0.031	0.037
Pseudacris triseriata (459)	-0.050	-0.032	-0.021
Pseudacris crucifer (459)	0.267**	0.257**	0.227**
Rana pipiens (459)	0.000	0.002	0.003
Rana palustris (459)	-0.043	-0.043	-0.043
Bufo americanus (459)	-0.021	-0.010	-0.002
Hyla versicolor/chrysoscelis (459)	0.092*	0.077	0.069
Acris crepitans blanchardi (459)	0.123**	0.127**	0.129**
Rana clamitans (459)	0.139**	0.173**	0.172**
Rana catesbeiana (459)	0.183**	0.196**	0.198**

Table 1.10

Correlations between cumulative monthly precipitation prior to and during breeding period and each species' route variables. Values are Spearman rank correlation coefficients (r_s; *$p<0.05$, **$p<0.01$). Sample size for each pairwise comparison is the same for all species (except *Bufo fowleri*) for any given month and is given in the bottom two rows of the table.

	February	March	April	May	June	July
Bufo fowleri						
Frequency	0.032	0.053	-0.014	-0.051	-0.014	
Index	0.031	0.053	-0.011	-0.054	-0.014	
Adjusted Index	0.030	0.053	-0.010	-0.054	-0.013	
Rana sylvatica						
Frequency	-0.009	-0.113*	-0.009			
Index	0.010	-0.113*	0.005			
Adjusted Index	0.017	-0.115**	0.007			
Pseudacris triseriata						
Frequency	0.105*	0.060	0.051	0.022		
Index	0.096*	0.047	0.056	0.049		
Adjusted Index	0.087	0.033	0.058	0.067		
Pseudacris crucifer						
Frequency	0.103*	0.025	-0.019	0.038		
Index	0.073	0.010	0.034	0.052		
Adjusted Index	0.055	0.007	0.051	0.046		
Rana pipiens						
Frequency	-0.075	0.001	0.044	-0.065		
Index	-0.083	0.005	0.043	-0.075		
Adjusted Index	-0.086	0.004	0.043	-0.078		
Rana palustris						
Frequency	-0.093*	0.008	0.013	-0.023		
Index	-0.093*	0.008	0.013	-0.025		
Adjusted Index	-0.093*	0.008	0.014	-0.025		
Bufo americanus						
Frequency	0.048	0.035	-0.042	0.089*		
Index	0.020	0.019	-0.023	0.082		
Adjusted Index	0.002	0.014	-0.013	0.072		
Hyla versicolor/						
chrysoscelis	0.102*	-0.063	-0.048	0.078	0.036	
Frequency	0.081	-0.066	-0.043	0.114*	0.049	
Index	0.067	-0.049	-0.045	0.110*	0.054	
Adjusted Index						
Acris crepitans						
blanchardi	0.082	0.087	-0.053	-0.027	-0.035	-0.084
Frequency	0.083	0.086	-0.053	-0.026	-0.033	-0.084
Index	0.084	0.085	-0.054	-0.026	-0.032	-0.084
Adjusted Index						

Rana clamitans	0.135**	0.036	-0.097*	0.021	-0.087	-0.126**
Frequency	0.173**	0.059	-0.108*	0.003	-0.106*	-0.137**
Index	0.176**	0.051	-0.093*	-0.004	-0.101*	-0.132**
Adjusted Index						
Rana catesbeiana						
Frequency	0.056	0.024	-0.050	0.053	-0.007	0.029
Index	0.063	0.019	-0.008	0.045	0.011	0.059
Adjusted Index	0.058	0.019	-0.006	0.040	0.009	0.061
N; *Bufo fowleri*	253	253	256	261	259	256
N; all other species	575	578	582	583	575	566

Table 1.11

Correlations between mean monthly temperature during the breeding period and each species' route variables. Values are Spearman rank correlation coefficients (r_s; *$p<0.05$, **$p<0.01$). Sample size for each pairwise comparison is the same for all species (except *Bufo fowleri*) for any given month and is given in the bottom two rows of the table.

	February	March	April	May	June	July
Bufo fowleri						
Frequency		0.016	-0.105	-0.042	-0.106	
Index		0.015	-0.105	-0.040	-0.106	
Adjusted Index		0.015	-0.105	-0.040	-0.107	
Rana sylvatica						
Frequency	-0.176**	-0.268**	-0.008			
Index	-0.165**	-0.274**	0.021			
Adjusted Index	-0.158**	-0.273**	0.035			
Pseudacris triseriata						
Frequency	0.062	0.063	0.108*	0.020		
Index	0.035	0.039	0.099*	0.016		
Adjusted Index	0.017	0.023	0.096*	0.019		
Pseudacris crucifer						
Frequency	-0.066	-0.095*	-0.027	-0.071		
Index	-0.050	-0.098*	0.008	-0.045		
Adjusted Index	-0.036	-0.087	0.020	-0.031		
Rana pipiens						
Frequency		-0.019	-0.032	-0.002		
Index		-0.026	-0.036	-0.002		
Adjusted Index		-0.031	-0.037	-0.003		
Rana palustris						
Frequency		-0.041	-0.070	-0.033		
Index		-0.041	-0.070	-0.033		
Adjusted Index		-0.041	-0.070	-0.033		
Bufo americanus						
Frequency			-0.082	-0.140**		
Index			-0.095*	-0.141**		
Adjusted Index			-0.090*	-0.129**		
Hyla versicolor/ chrysoscelis			-0.039	-0.138**	-0.109*	
Frequency			-0.013	-0.147**	-0.080	
Index			-0.004	-0.137**	-0.062	
Adjusted Index						
Acris crepitans blanchardi				-0.005	0.000	0.032
Frequency				-0.008	0.000	0.032
Index				-0.009	0.000	0.032
Adjusted Index						
Rana clamitans						
Frequency				0.001	-0.062	0.068
Index				0.000	-0.037	0.107*

Adjusted Index				-0.008	-0.018	0.120**
Rana catesbeiana						
Frequency				-0.090*	-0.002	0.007
Index				-0.046	-0.051	0.034
Adjusted Index				-0.049	-0.053	0.035
N; *Bufo fowleri*		237	242	246	244	
N; all other species	524	526	534	540	533	519

Table 1.12

Results of route frequency regressions. Sample size indicates the number of routes used for analysis for each species for all route regression dependent variables. Mean trends (slopes of regressions in units of change in frequency per year) and associated 95% confidence intervals indicate the direction and magnitude of the annual rate of change, P values indicate whether trend (slope) differed significantly from zero.

Species	**N**	**Mean trend**	**Lower CI**	**Upper CI**	**P value**
Bufo fowleri	25	-0.037	-0.084	0.010	0.120
Rana sylvatica	132	-0.007	-0.032	0.017	0.560
Pseudacris triseriata	133	0.009	-0.004	0.022	0.184
Pseudacris crucifer	130	-0.002	-0.009	0.005	0.612
Rana pipiens	115	-0.017	-0.038	0.004	0.111
Rana palustris	35	-0.039	-0.083	0.004	0.077
Bufo americanus	130	-0.002	-0.021	0.017	0.819
Hyla versicolor/chrysoscelis	131	-0.015	-0.026	-0.004	0.010
Acris crepitans blanchardi	21	-0.018	-0.046	0.009	0.173
Rana clamitans	132	0.000	-0.010	0.009	0.920
Rana catesbeiana	109	0.017	0.002	0.033	0.028

Table 1.13

Results of route index regressions. Mean trends (slopes of regressions in units of change in route index per year) and associated 95% confidence intervals indicate the direction and magnitude of the annual rate of change, P values indicate whether trend (slope) differed significantly from zero.

Species	**Mean trend**	**Lower CI**	**Upper CI**	**P value**
Bufo fowleri	-0.043	-0.098	0.013	0.124
Rana sylvatica	0.006	-0.021	0.032	0.677
Pseudacris triseriata	0.009	-0.008	0.026	0.293
Pseudacris crucifer	-0.002	-0.010	0.006	0.597
Rana pipiens	-0.018	-0.041	0.005	0.116
Rana palustris	-0.039	-0.089	0.012	0.127
Bufo americanus	-0.004	-0.027	0.019	0.721
Hyla versicolor/chrysoscelis	-0.017	-0.031	-0.004	0.014
Acris crepitans blanchardi	-0.017	-0.05	0.016	0.304
Rana clamitans	0.003	-0.008	0.014	0.591
Rana catesbeiana	0.019	0.003	0.035	0.012

Table 1.14

Results of route adjusted index regressions. Mean trends (slopes of regressions in units of change in adjusted index per year) and associated 95% confidence intervals indicate the direction and magnitude of the annual rate of change, P values indicate whether trend (slope) differed significantly from zero.

Species	**Mean trend**	**Lower CI**	**Upper CI**	**P value**
Bufo fowleri	-0.076	-0.163	0.011	0.937
Rana sylvatica	-0.003	-0.048	0.041	0.894
Pseudacris triseriata	0.013	-0.013	0.040	0.324
Pseudacris crucifer	-0.001	-0.013	0.011	0.873
Rana pipiens	-0.027	-0.062	0.008	0.136
Rana palustris	-0.064	-0.146	0.018	0.121
Bufo americanus	-0.009	-0.044	0.026	0.604
Hyla versicolor/chrysoscelis	-0.028	-0.049	-0.008	0.007
Acris crepitans blanchardi	-0.028	-0.083	0.026	0.289
Rana clamitans	0.005	-0.011	0.021	0.561
Rana catesbeiana	0.033	0.007	0.058	0.012

Table 1.15

Results of repeated measures analyses of variance for routes for which the same volunteers submitted data for each year 1996-2002. Sample size is the same for all species (n = 20) except *Bufo fowleri* (n = 12). See text for explanation of dependent variables (route frequency, route index, and adjusted route index).

Species	**F**	**P Value**	**Polynomial Trend**	**P Value**
1. Route Frequency				
Bufo fowleri	1.370	0.260		
Rana sylvatica	2.232	0.045	2	0.047
Pseudacris triseriata	1.070	0.381		
Pseudacris crucifer	2.574	0.037	2	0.011
Rana pipiens	0.599	0.721		
Bufo americanus	1.460	0.198		
Hyla versicolor/chrysoscelis	2.997	0.025	2	0.048
Rana clamitans	2.681	0.031	5	0.025
Rana catesbeiana	1.902	0.090	1	0.025
2. Route Index				
Bufo fowleri	1.575	0.186		
Rana sylvatica	2.614	0.021	5	0.011
Pseudacris triseriata	1.410	0.222		
Pseudacris crucifer	2.743	0.028	2	0.001
Rana pipiens	0.924	0.476		
Bufo americanus	1.254	0.284		
Hyla versicolor/chrysoscelis	2.321	0.056		
Rana clamitans	4.375	0.002	1	0.046
Rana catesbeiana	1.645	0.141		
3. Adjusted Route Index				
Bufo fowleri	1.670	0.166		
Rana sylvatica	2.565	0.023	5	0.015
Pseudacris triseriata	1.569	0.172		
Pseudacris crucifer	2.107	0.074		
Rana pipiens	0.915	0.482		
Bufo americanus	1.212	0.305		
Hyla versicolor/chrysoscelis	1.958	0.108		
Rana clamitans	4.256	0.004	1	0.046
Rana catesbeiana	1.530	0.174		

Figure 1.1

Calling calendar for frogs and toads of southern Michigan. Arrows represent approximate beginning, ending, and duration of calling period for males of each species. Breeding effort is largely dependent on weather conditions; dates are extremely variable and dependent on temperature and precipitation each year. Figure courtesy of Lori G. Sargent (MDNR, MFTS coordinator).

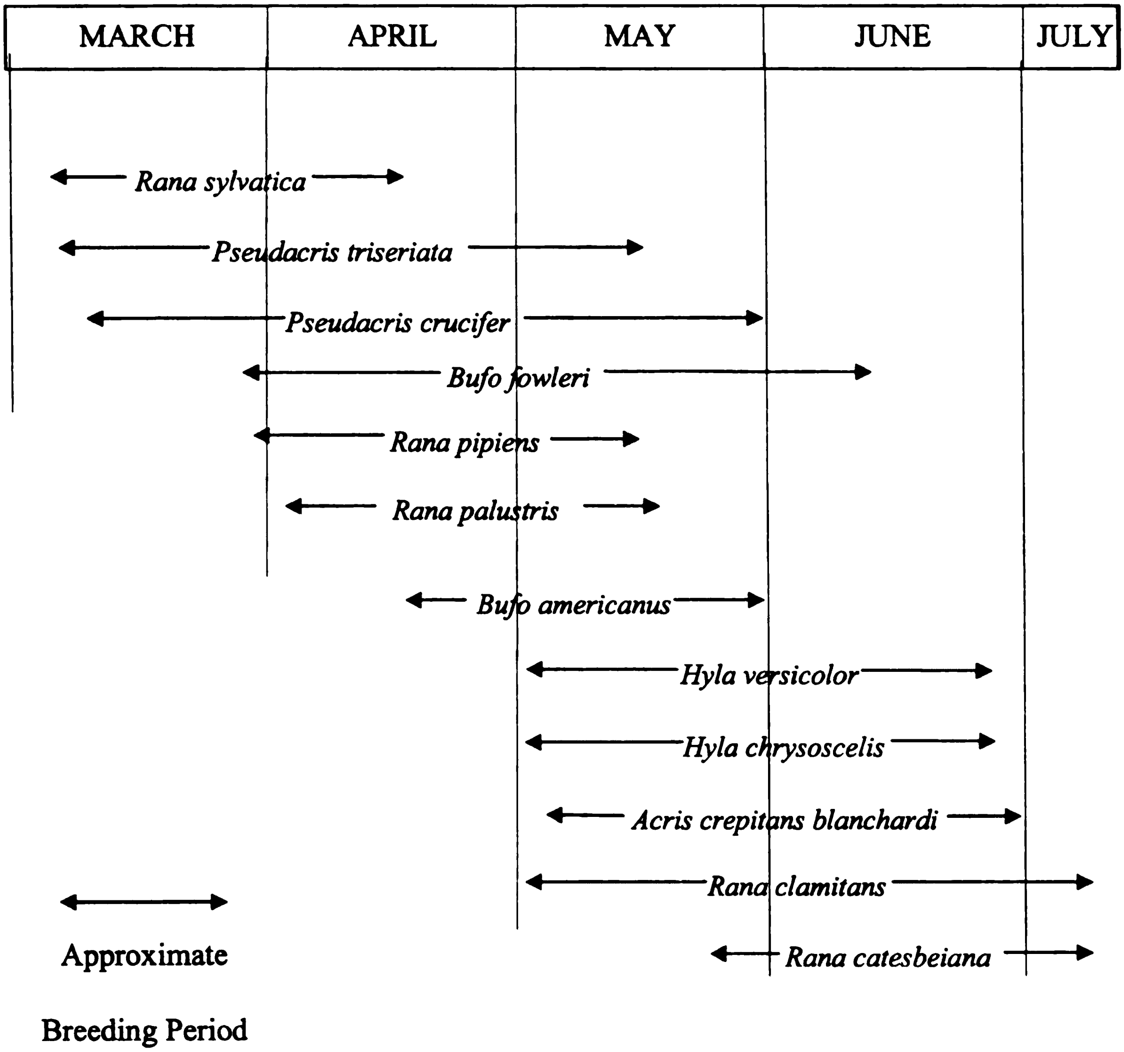


Figure 1.2

Distribution of MFTS routes in Michigan. The box represents the region evaluated in detail in this study. Each point represents a route comprised of 10 survey sites at anuran breeding ponds.

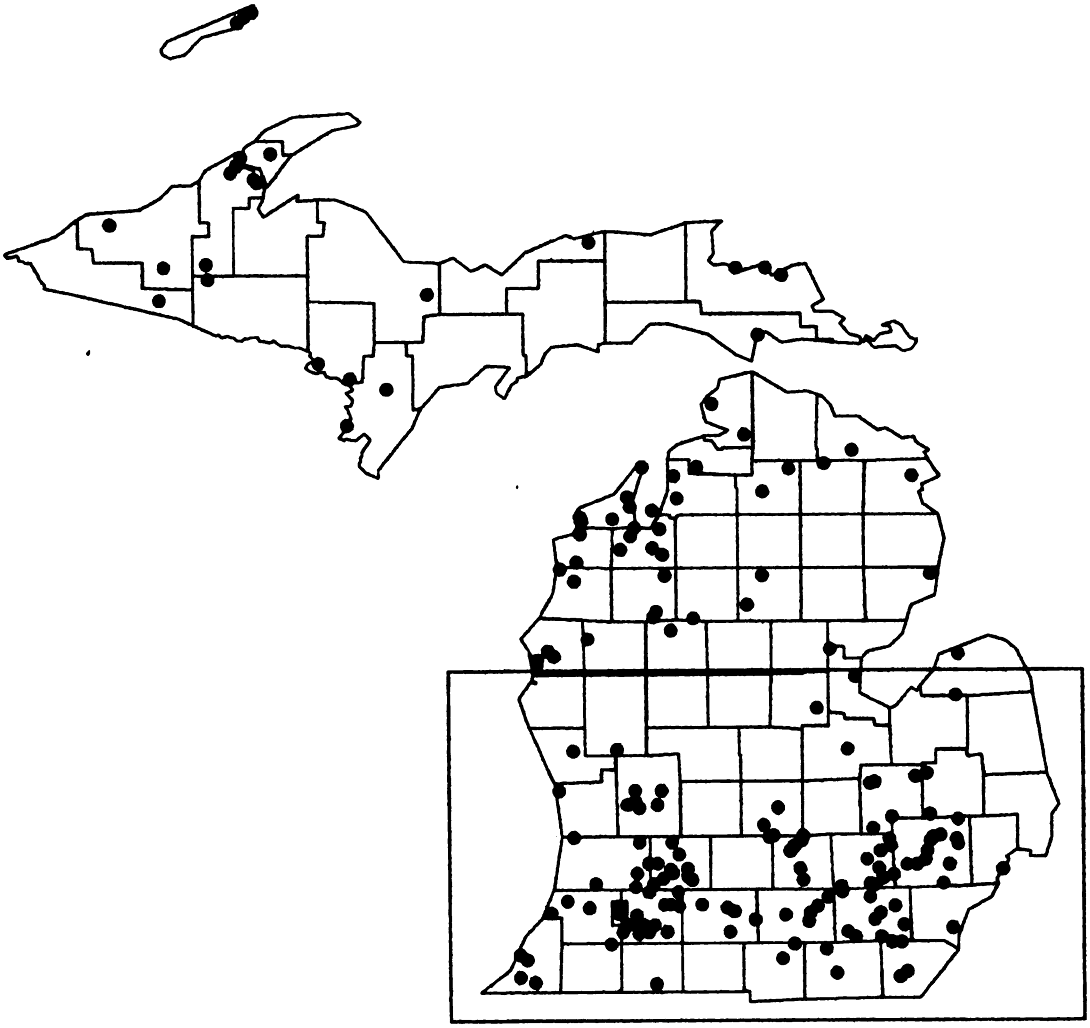


Figure 1.3

Location of climate stations used for temperature and precipitation in southern Michigan. Daily temperature and precipitation data were obtained for these sites for 1995-2002 and matched to the nearest MFTS route.

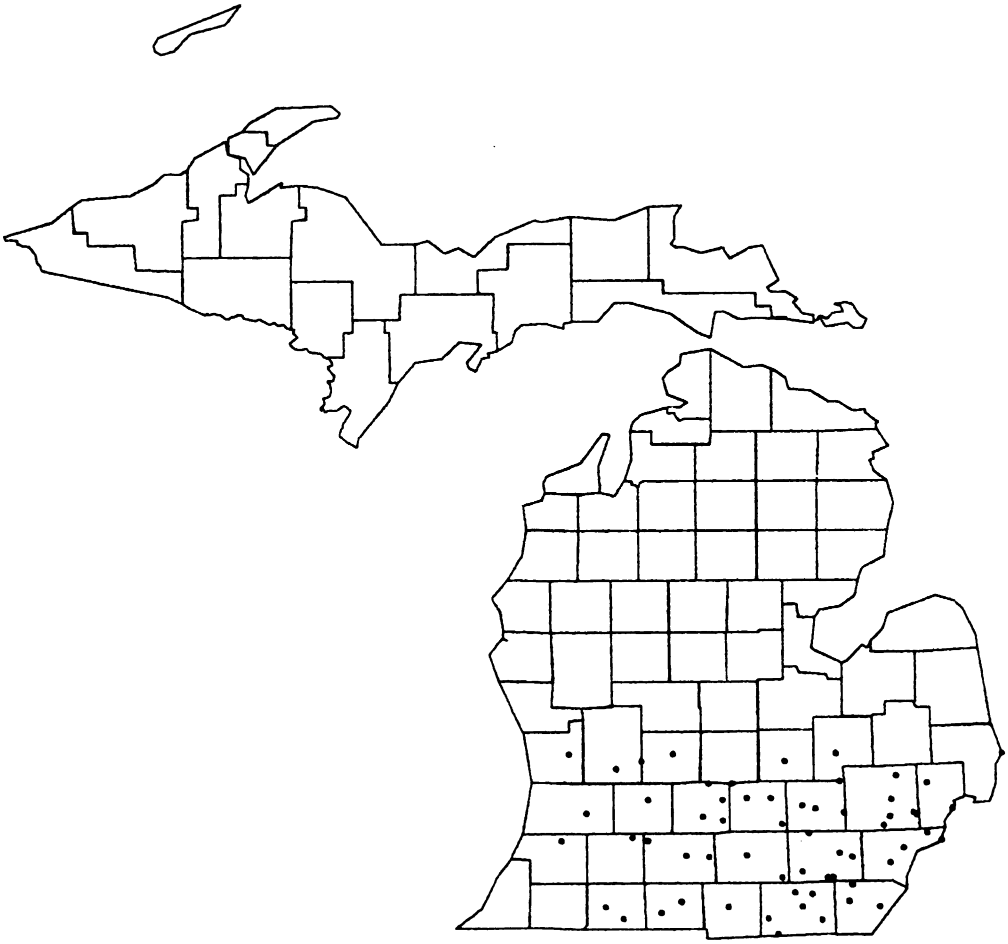


Figure 1.4

Year of route establishment. There were a total of 269 routes in southern lower Michigan. Each bar represents the proportion that was established in each year of the MFTS.

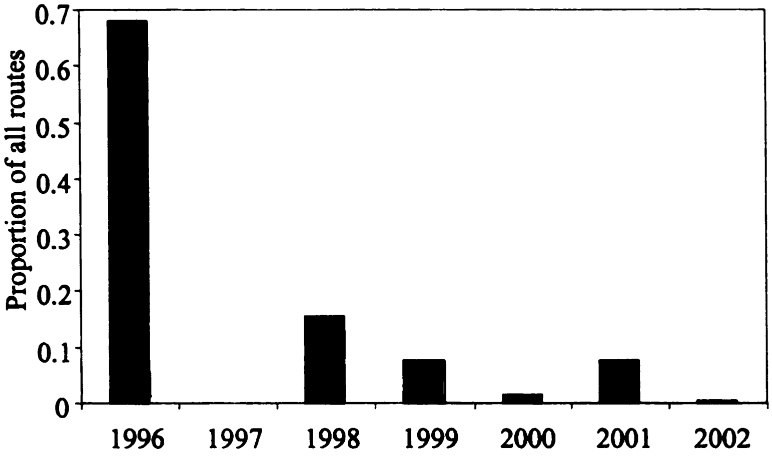


Figure 1.5

Number of years routes have been surveyed. Bars represent the proportion of the 269 total routes in southern lower Michigan that was surveyed for a given time period.

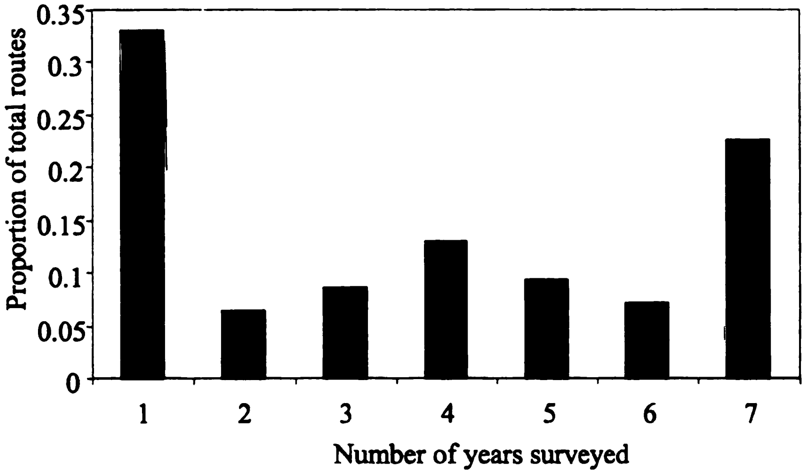


Figure 1.6

Patterns of temperature and precipitation during anuran breeding season, 1996-2002. (A) Monthly mean low temperature, (B) Monthly mean high temperature, (C) Monthly mean daily temperature, (D) Monthly mean precipitation. All data represent means ± SE. Asterisks represent significance level of statistical tests (*$p<0.05$, **$p<0.01$, ***$p<0.005$, ****$p<0.001$).

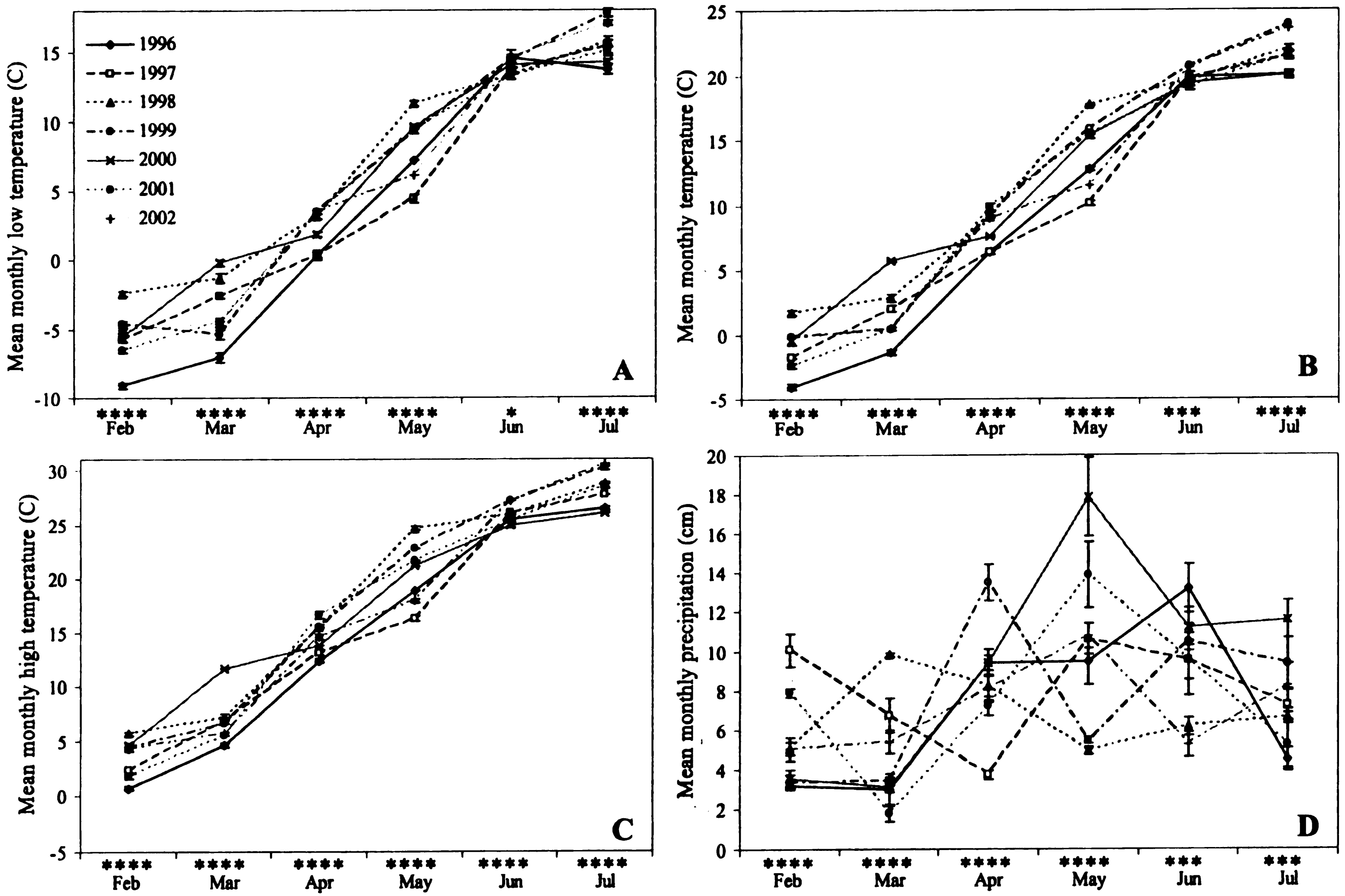
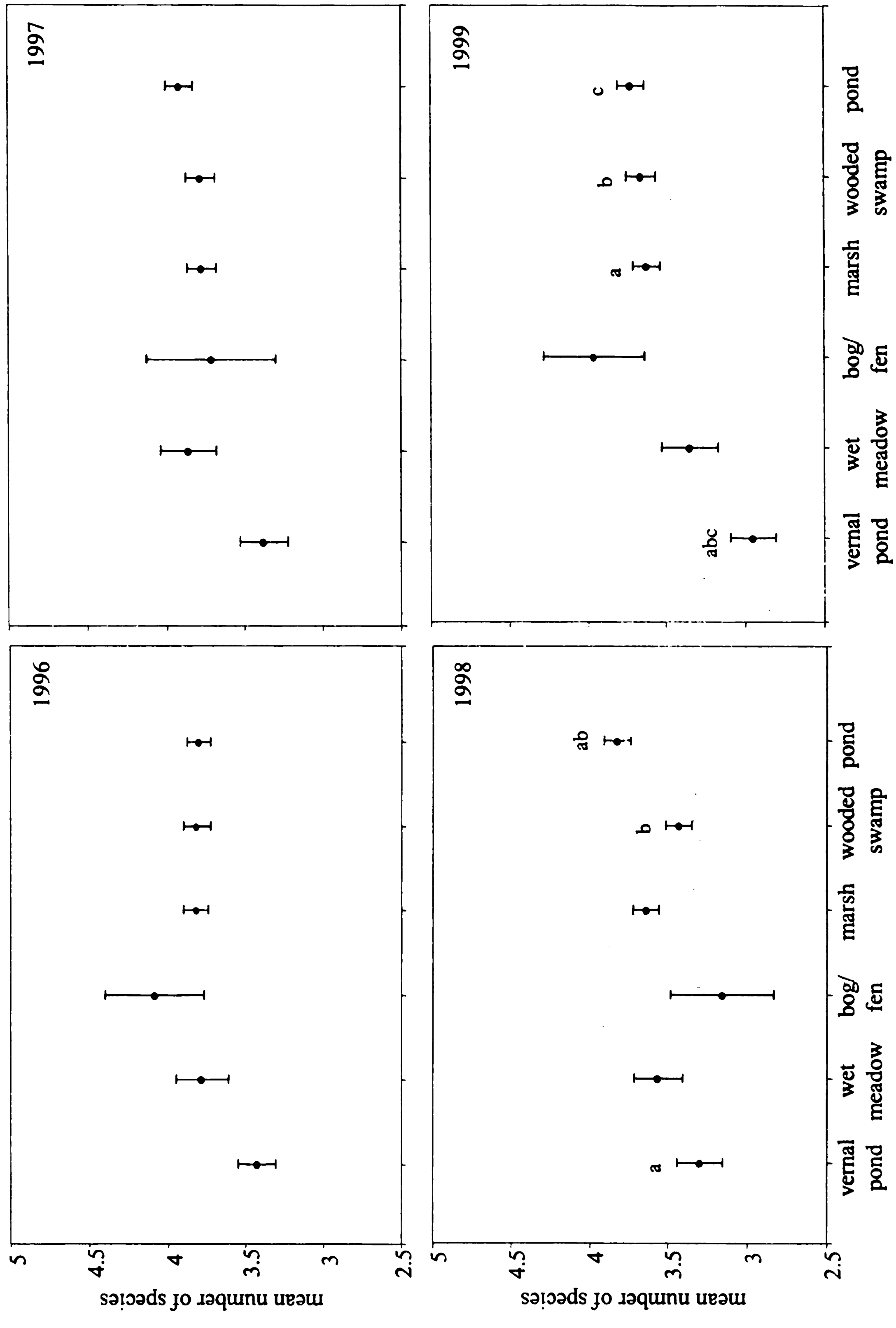

1996
1997
1998
1999
2000
2001
2002
Mean monthly low temperature (C)
15
10
5
0
-5
-10
A
**** **** **** **** * ****
Feb Mar Apr May Jun Jul
Mean monthly temperature (C)
25
20
15
10
5
0
-5
B
**** **** **** **** *** ****
Feb Mar Apr May Jun Jul
Mean monthly high temperature (C)
30
25
20
15
10
5
0
-5
C
**** **** **** **** **** ****
Feb Mar Apr May Jun Jul
Mean monthly precipitation (cm)
20
18
16
14
12
10
8
6
4
2
0
D
**** **** **** **** *** ***
Feb Mar Apr May Jun Jul

Figure 1.7

Mean number of species (+/- SE) present in wetland types in each year. Each panel represents a single year of MFTS data (year given in upper right corner of each panel). Horizontal and vertical axes are identical on all panels, and axis labels are provided along the left and bottom margins for all panels. Points with matching letters indicate significant pairwise differences (Bonferroni corrected pairwise comparisons, $p < 0.05$).


1996
1997
1998
1999
mean number of species
mean number of species
5
4.5
4
3.5
3
2.5
vernal pond
wet meadow
bog/ fen
marsh
wooded swamp
pond
a
b
ab
abc
a
b
c

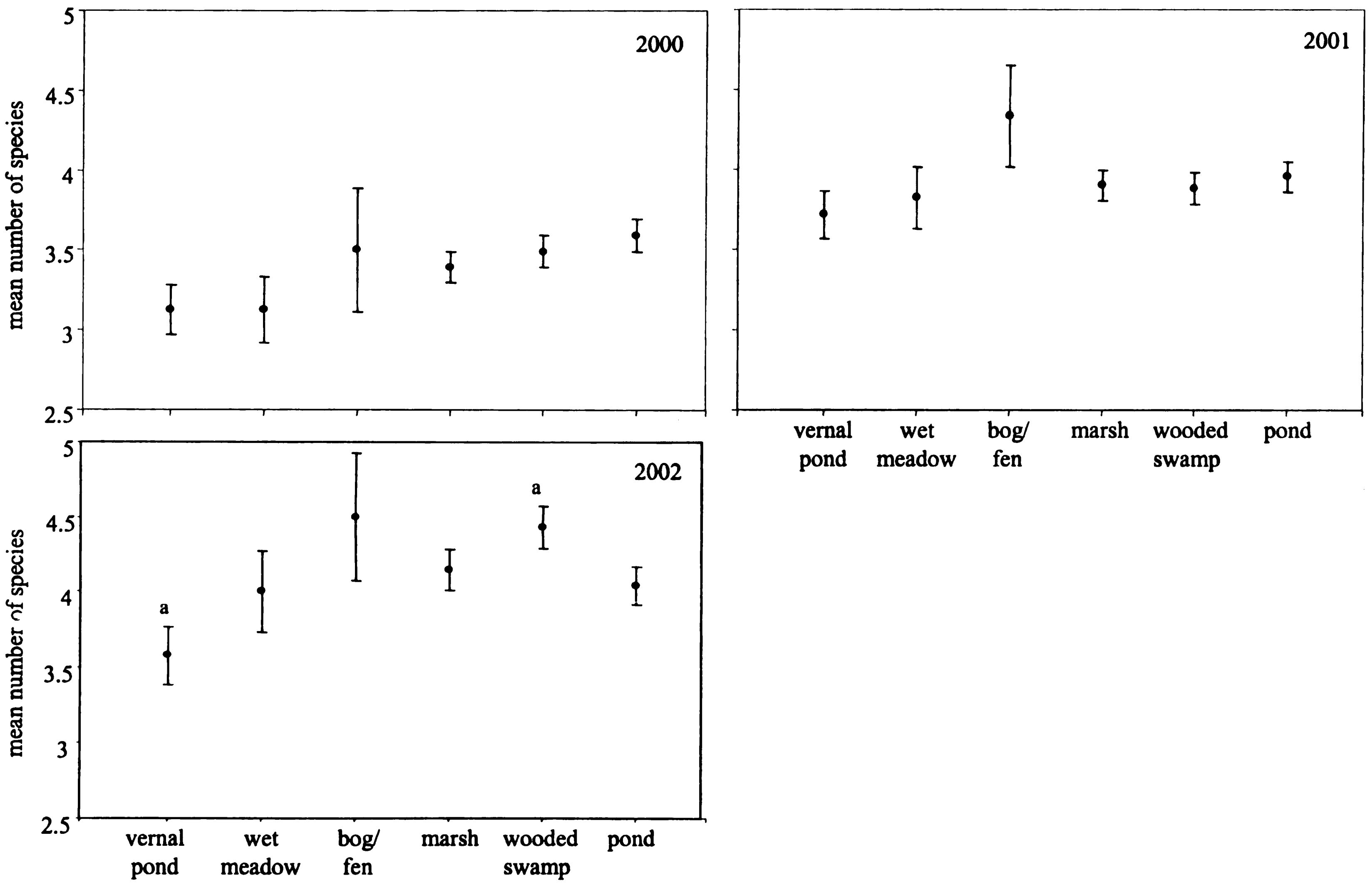

2000
2001
2002
mean number of species
5
4.5
4
3.5
3
2.5
vernal pond
wet meadow
bog/ fen
marsh
wooded swamp
pond
a
a

Figure 1.8

Mean number of anuran species detected calling (+/- SE) in each wetland type from 1996 – 2002. (A) Woody vegetation dominated wetland communities, (B) Herbaceous vegetation/open water dominated wetland communities.

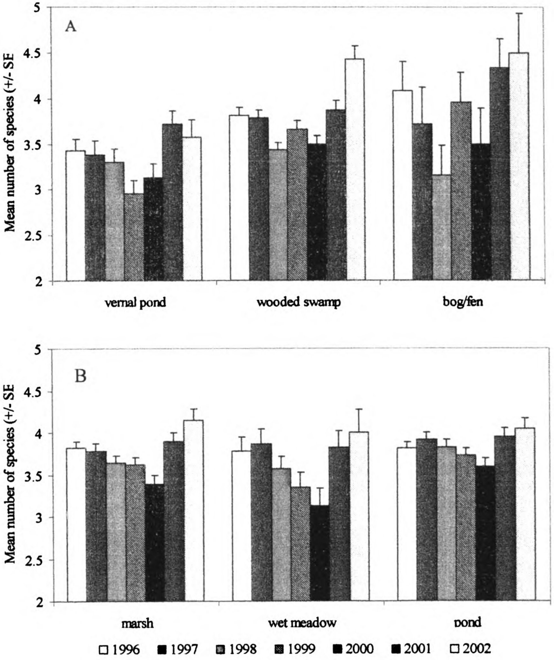
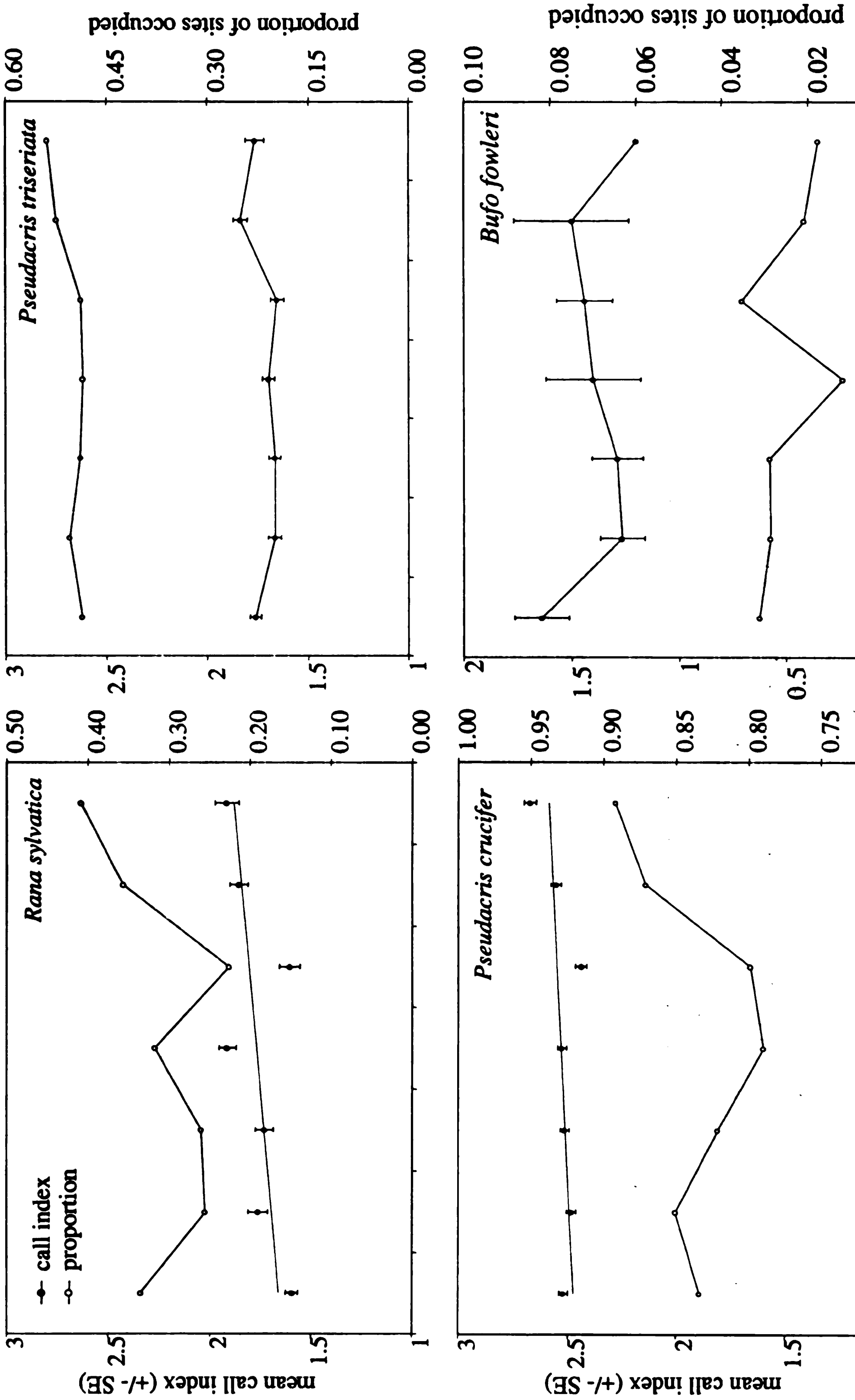
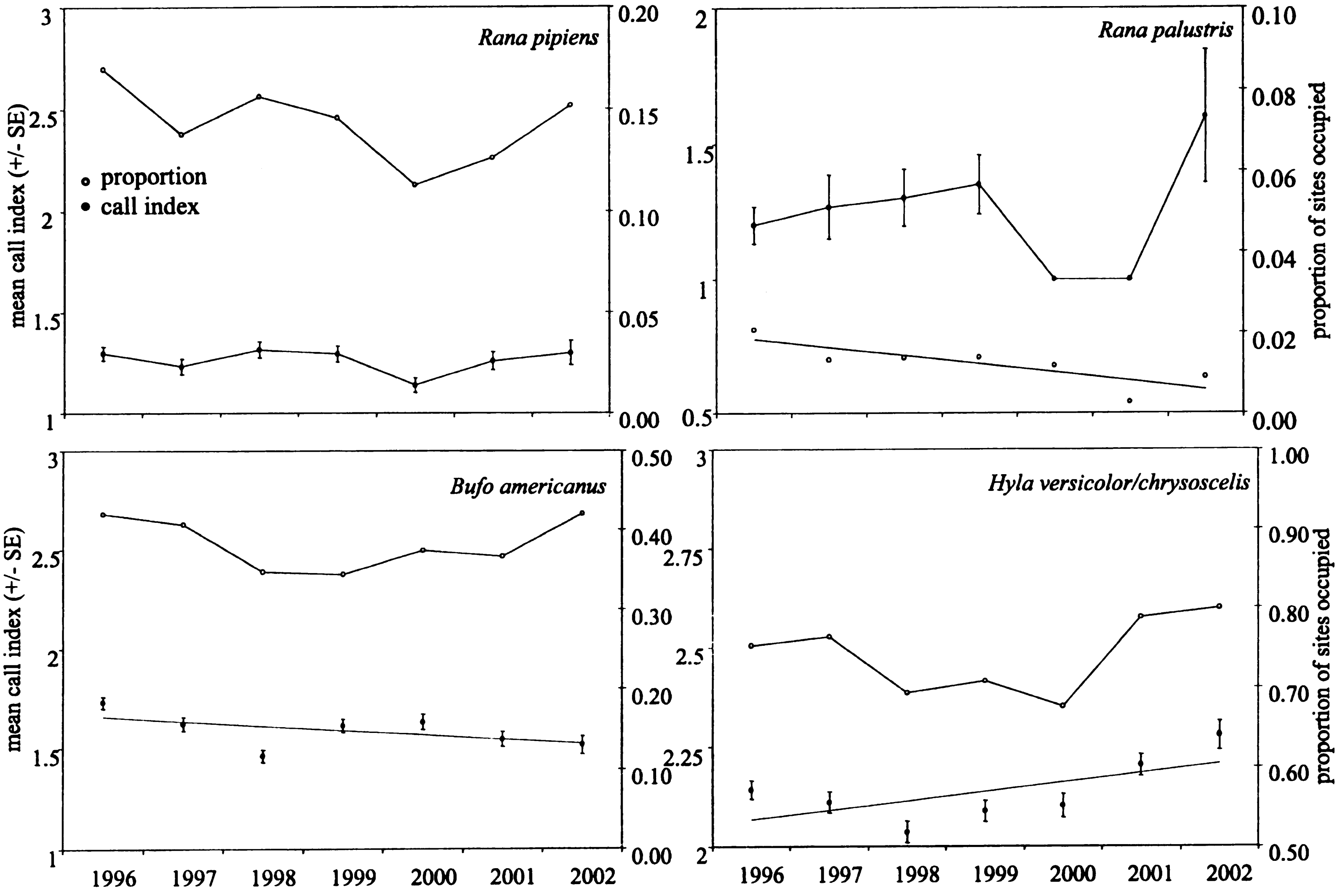
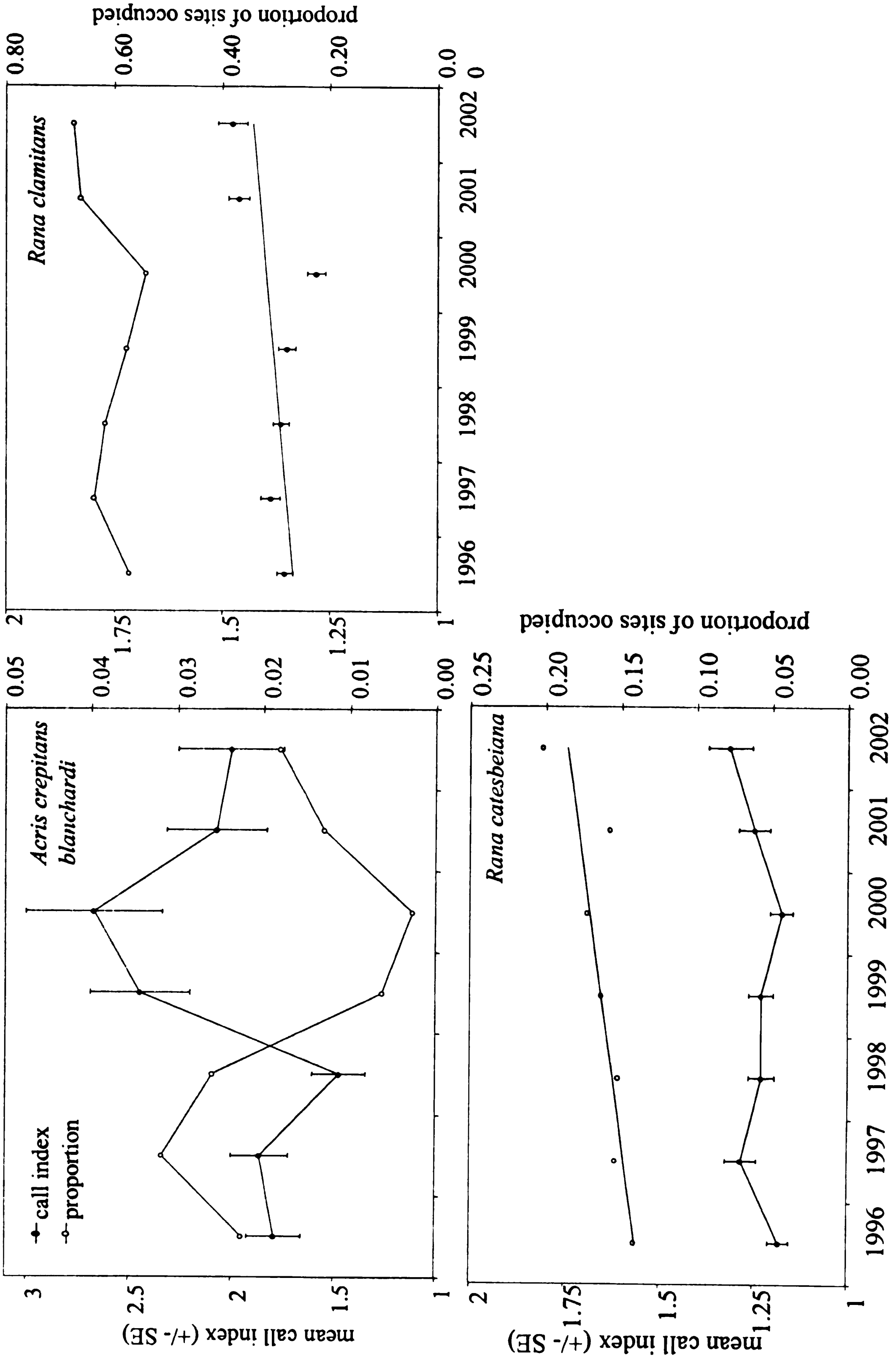


Figure 1.9

Site occupancy and mean call index values (+/- SE) for each species. Each panel represents one species (species indicated in upper right corner of each panel). Open circles indicate proportion of sites occupied by each species, black circles indicate mean annual call index value. Mean annual call index values are plotted on the primary vertical axis, and site occupancy is plotted on the secondary vertical axis. Axis labels are identical for all panels and are provided at the outer margins. Significant linear relationships are indicated with trendlines. See Tables 1.6 – 1.7 and Results section for statistical analyses.

Rana sylvatica
call index
proportion
Pseudacris triseriata
Pseudacris crucifer
Bufo fowleri
mean call index (+/- SE)
proportion of sites occupied
1996
1997
1998
1999
2000
2001
2002
3
2.5
2
1.5
1
0.5
0
0.50
0.40
0.30
0.20
0.10
0.00
0.60
0.45
0.15
1.00
0.95
0.90
0.85
0.80
0.75
0.70
0.08
0.06
0.04
0.02


Rana pipiens
Rana palustris
Bufo americanus
Hyla versicolor/chrysoscelis
o proportion
• call index
mean call index (+/- SE)
proportion of sites occupied
1
1.5
2
2.5
3
0.5
2.25
2.75
0.00
0.05
0.10
0.15
0.20
0.02
0.04
0.06
0.08
0.30
0.40
0.50
0.60
0.70
0.80
0.90
1.00
1996
1997
1998
1999
2000
2001
2002


call index
proportion
Acris crepitans blanchardi
Rana clamitans
Rana catesbeiana
mean call index (+/- SE)
proportion of sites occupied
1996
1997
1998
1999
2000
2001
2002
3
2.5
2
1.5
1
1.75
1.25
0.05
0.04
0.03
0.02
0.01
0.00
0.80
0.60
0.40
0.20
0.0
0
0.25
0.20
0.15
0.10
0.05

Chapter Two

Evaluation of methods and data quality from a volunteer-based amphibian call survey

Abstract

The Michigan Frog and Toad Survey (MFTS) is an annual volunteer-based anuran census. One major concern with data collected by volunteers is its quality and consistency. The goal of this study was to evaluate the effect of observer experience on data quality. Questionnaires and an audio CD with a simulated anuran survey route were mailed to all active volunteers. We were able to determine volunteer demographics and commitment to program; species characteristically missed, misidentified, over or underestimated; and influence of volunteer background on data quality. Volunteers were reasonably reliable in their abilities to determine species presence, but there was extensive variability in abundance estimation. Some species were characteristically confused by volunteers, and additional species were frequently recorded even when absent from a site. Prior experience and background had little influence in the ability to identify or estimate abundance of calling frogs. Our results indicate that such survey approaches are easy for volunteers to learn and provide reasonable estimates for species' presence, but do not necessarily estimate abundance well. These results will be used to improve data collection protocols for the MFTS and better analyze and interpret the data collected, and could also be beneficial for other regional amphibian monitoring programs.

Introduction

In the last decade, there has been increased interest, debate, and research concerning the apparent global declines of amphibian populations, although the causes have yet to be unambiguously determined (Blaustein et al. 1994a, Sarkar 1996, Green 1997b, Alford and Richards 1999). The primary obstacle that must be overcome in evaluating potential amphibian declines is separating effects due to anthropogenic influences from natural population fluctuations (Pechmann and Wilbur 1994, Travis 1994). To do this, long-term data from extensive areas are needed (Blaustein et al. 1994a), and regional amphibian monitoring programs can contribute such information.

Surveys of calling anurans (hereafter call surveys) are being used for amphibian monitoring in many states and Canadian provinces (e.g., Huff 1991, Bishop et al. 1997, Lepage et al. 1997, Mossman et al. 1998), and have the potential to provide valuable information about population size and status (Zimmerman 1994, Shirose et al. 1997, Driscoll 1998). The North American Amphibian Monitoring Program (NAAMP) has developed a unified protocol for volunteer-based call surveys that has been implemented in 24 states (Weir and Mossman, in press). This technique provides a fairly efficient and effective method of surveying anurans over large geographical regions (Scott and Woodward 1994), and has successfully allowed collection of data on presence and abundance of frogs and toads in many areas. Call survey protocols are easy for volunteers to learn, and also provide an excellent means for promoting education about wetlands and amphibian conservation.

Annual monitoring data for Michigan's 13 species of frogs and toads can be used to evaluate short-term trends in population dynamics and help to guide research and conservation efforts for these species. The Michigan Frog and Toad Survey (MFTS) protocol was originally modified from that developed for the Wisconsin Department of Natural Resources (WDNR) frog survey (Mossman et al. 1998). The first surveys in Michigan were done in 1988 on a limited basis and were discontinued a few years later due to lack of personnel to coordinate the survey. In 1996, the Michigan Department of Natural Resources (MDNR) initiated a statewide annual frog and toad survey that uses a network of volunteer observers to monitor breeding anuran populations (Sargent 2000). NAAMP developed survey protocols in 1995, but these were not approved for national use until 2000 (Weir and Mossman, in press). Since routes had already been established in Michigan, and data had already been submitted for five years by the time the NAAMP protocols were officially available, the MFTS continued to use the original protocols. However, some MFTS routes adhere to NAAMP protocols, and these data are submitted for use at state and national levels. In the MFTS, volunteers establish routes by first submitting a map and descriptions of a series of 12 potential wetland survey sites identified without knowledge of wetlands or presence of amphibians (i.e., sites identified in winter or otherwise outside the breeding season when anurans are inactive); upon approval of the MDNR state coordinator the route is driven and sites are established (Sargent 2000). NAAMP routes use randomly generated driving maps (Weir and Mossman, in press). The volunteers survey routes 3 times each spring, corresponding to peak breeding times of anurans, and record the identity of each species and an index of their calling intensity (0 = absent, 1 = few individuals with non-overlapping calls, 2 = many individuals with overlapping but distinguishable calls, 3 = full chorus with individual calls indistinguishable). MFTS protocols instruct volunteers to begin surveying their routes 30 minutes after sunset and to listen for 5 minutes at each site (Sargent 2000).

Volunteer training is an important component that contributes to the success of a regional monitoring program. Prior to onset of data collection in 1996 and again in 2001, training workshops were held throughout the state. These training workshops provided information on general frog biology and habitat requirements, how to distinguish species by sight and sound, and instructions for establishing a route and conducting the survey (Sargent 2000). In addition to these initial training workshops, instructional packets that included information on protocols and a training cassette with examples of all species' calls were distributed to interested participants.

Several factors (e.g., prior experience or hearing ability) may influence observers' abilities to correctly identify anurans and estimate their abundance. Previous studies suggest that novice observers provide reliable data on species' presence, but their assignment of call index values is more variable (Bishop et al. 1997, Shirose et al. 1997, Hemesath 1998). Differences among observers could influence survey data quality, and should be incorporated into analyses of population changes (Sauer et al. 1994).

Because data for the MFTS are collected each year by hundreds of volunteers with varying expertise (range of 198-293 routes submitting data during 7 years of program; most routes had at least 2 volunteers), we initiated a study to identify factors that influenced data collection so that we could incorporate modifications to deal with these factors into data analyses. Although the problems of observer bias and subsequent data analyses have been investigated for monitoring programs such as the North American Breeding Bird Survey (BBS, Sauer et al. 1994, Link and Sauer 1996, Kendall et al. 1996), differences among volunteer observers and their implications for data analyses need to be more thoroughly addressed for amphibian monitoring programs (but see Bishop et al. 1997, Shirose et al. 1997, Hemesath 1998). Methods for assessing observer experience have been proposed (Bishop et al. 1997, Shirose et al. 1997, Hemesath 1998), but have not been widely implemented.

The overall goal of this study was to evaluate observer experience and data accuracy and precision for the MFTS. Based upon this goal, the primary objectives were to evaluate how volunteer background and experience influenced anuran identifications and assignment of call index values, determine implications of observer differences on analyses of population trends, and establish an observer evaluation process that could be implemented by other states with similar monitoring programs. This chapter represents collaboration with Lori G. Sargent, the State Coordinator for the MFTS (Genet and Sargent 2003).

Materials and Methods

We administered a mail survey between July and December of 2001. The survey was evaluated for ethical appropriateness by the Michigan State University Committee on Research Involving Human Subjects (UCRIHS IRB# 01-324). In mid-July we sent a questionnaire and audio CD to all MFTS volunteers who had submitted data in 1999 and/or 2000 (n = 355). We sent a second mailing of reminder/thank you postcards in early September, and we also provided additional questionnaires and/or CDs to volunteers who requested them at that time. Finally, we mailed the annual MFTS update in early December, which included a preliminary report of the survey data and encouragement to send in responses if volunteers had not already done so. We did not accept any responses after 31 December 2001. We removed from the sample surveys that were returned as undeliverable by the United States Postal Service or in cases where the recipient was deceased. We included surveys that were returned blank or with a note indicating no interest in participating in the survey in the sample size, but considered these non-responses (counted in final corrected sample size, but data omitted from analyses). Respondents provided information about basic demographics, participation, and experience with the MFTS and wildlife in general, and commitment to this and other wildlife monitoring programs on their questionnaires (specific questions from the questionnaire are found in Appendix A).

We also enclosed an audio CD with 12 tracks with the survey. Each track represented a wetland breeding site, typical of those visited by volunteers as they collect data for the MFTS. We instructed the volunteers to listen, and using data forms identical to those used for annual surveys, record each species and assign an abundance index for each CD track in the same manner as for the sites they monitor annually. Each track was 5 minutes in length, the recommended listening time for MFTS protocol (Sargent 2000).

If respondents failed to follow survey instructions or only submitted a partial questionnaire or datasheet, we edited the data as follows. If the respondent gave a range when asked for a numeric response, we assigned the arithmetic mean. In cases where respondents indicated they would submit data as long as possible in response to question 3 (Appendix A), we assigned a value of 10 years. We omitted non-responses on individual questions from analysis. We categorized observers as novice (n = 18), intermediate (n = 46), or expert (n = 90) based on the number of years they had submitted data to the MFTS (1 – 6 yrs.) and their perceived level of expertise (5-point rating scale, range 2 – 5). We summed these two values (summed score range: 3 – 11) and divided the resulting scores equally into the three experience categories: novice = 3 – 5, intermediate = 6 – 8, expert = 9 – 11. The call index values assigned by respondents were compared to the values independently predetermined by experts (both authors and two additional experts in the field) for each species on each of the 12 tracks. Statistical analyses were performed using appropriate statistical methods described in the following paragraphs (Zar 1998) using SAS statistical software (SAS Institute, Cary, NC).

We used chi-square analyses to test whether species identifications deviated from expected (i.e., all volunteers correctly identified all species on each track) and to determine whether respondents assigned the expected call index values (predetermined by authors and two other experts) for each species on each track. Volunteers in other regional call surveys have difficulty discriminating between the two highest call index values (L. B. Johnson, University of Minnesota Duluth, personal communication). Thus, 2 separate hypotheses were tested for each track of the CD: 1) respondents correctly assigned 4-category call index values (0, 1, 2, 3), and 2) respondents correctly assigned 3-category call index values (0, 1, 2+3 combined). For the three species with restricted distributions within Michigan (Fowler's toads, mink frogs, and Blanchard's cricket frogs), we used contingency table analyses to determine whether there was a significant association between living within a species' range and correct identification. We also used contingency table analyses to determine if observer experience level (novice, intermediate, or expert) influenced abundance estimation of each species (correct, over- or underestimation of abundance, based on authors' predetermined values). We used both parametric and non-parametric (Kruskal-Wallis) analysis of variance (ANOVA) to determine whether observer experience influenced correct identification of species. Nonparametric tests were implemented in the cases where data did not meet assumptions of parametric tests (i.e., small sample size). Data are reported as means ± SE unless otherwise noted, and a P-value < 0.05 is considered statistically significant.

Results

Volunteer Demographics

Of the 355 questionnaires sent to volunteers, 4 were undeliverable, 1 recipient was deceased, and 179 were returned, yielding a 51.1% response rate (corrected sample size, n = 350). Volunteers indicated extensive experience with wildlife and commitment to this program (Table 2.1). The typical respondent was just over 50 years old, and 26% of respondents were retired. Slightly more females (53.7%) than males (46.3%) participated in this project, although the difference was not significant ($\chi^2_1 = 0.5746$, $P = 0.464$). Over 70% of respondents were also avid birders, and 44% were involved in at least one additional wildlife monitoring program.

The typical respondent felt he or she had improved approximately 2 points on a rating scale from 1 (low) to 5 (high) from beginning in the MFTS to their current level of expertise (beginning: 1.66 ± 0.07, current: 3.56 ± 0.05). With respect to training, volunteers predominantly listened to the training tape (97.7%) and attended training workshops (66.5%). The majority of volunteers participated in more than one type of training activity (82.4%), but fewer practiced in the field (11.4%) or participated in some other type of training activity (33.0%). On average, two people participated in each survey route, and in > 85% of the cases, the number and identity of those people was consistent from year to year. Most respondents (80%) indicated that a primary observer had been designated for their route (if > 1 observer on that route). The primary observer was responsible for the data forms and establishing consensus when there were discrepancies among observers. Thirty-five percent of the respondents indicated that there had been discrepancies among observers in terms of species heard or call index values to be assigned. The most common methods for resolving these discrepancies were to discuss among observers until consensus was reached (58.3%), listen longer at the site (51.7%), check calls against the training tape (28.3%), and/or allow primary observer to make decision (8.3%).

Species Identification

Volunteers were able to identify species by their calls (Table 2.2, 2.3), but correct identifications varied from 60% for Fowler's toads (*Bufo fowleri*) to > 98% for northern green frogs (*Rana clamitans melanota*) and bullfrogs (*Rana catesbeiana*). The majority of species on a track were correctly identified by ≥ 80% of volunteers (Table 2.2, 2.3). Many respondents confused northern leopard frogs (*Rana pipiens*) and pickerel frogs (*Rana palustris*) (> 10%, Table 2.2). Fowler's toads were correctly identified by only 60% of the respondents (Table 2.2), and a large proportion of respondents indicated the presence of one (or both) of the gray treefrog species (*Hyla versicolor, H. chrysoscelis*) either instead of or in addition to Fowler's toads. Several respondents also confused the calls of mink frogs (*Rana septentionalis*) and wood frogs (*Rana sylvatica*) (Table 2.2). No other species appeared to be characteristically misidentified or confused with a similar-sounding species.

On 6 of the 12 tracks, volunteers' responses significantly differed from correct identifications ($P < 0.005$), indicating that they missed or misidentified a significant number of species. For the remaining tracks, volunteers correctly identified all species present, however, additional species not calling on the CD were also recorded (Table 2.2, 2.3). For the three species with restricted ranges, living within the species' range did not affect the observers' abilities to correctly identify these species (Table 2.4, $P > 0.05$). Novice, intermediate, and expert observers did not differ significantly in their abilities to correctly identify species' presence based on their calls ($H_2 = 1.468$, $P = 0.480$). Respondents in all three experience categories recorded correct identifications of all species combined (i.e., all species calling in concert at a breeding site) in > 85% of cases. Observer experience level also had no significant influence on respondents' abilities to correctly identify individual species ($P > 0.05$).

Abundance Estimation

There were discrepancies in assignment of call indices for some species even among respondents who correctly identified the species on each track of the CD recording. In many cases, there was consensus among respondents, but in others, respondents were relatively equally split among different call index values (Figure 2.1). For example, spring peepers (*Pseudacris crucifer*) were almost unanimously assigned call index 3 on track 1 (Figure 2.1a), while Blanchard's cricket frogs (*Acris crepitans blanchardi*) and green frogs were almost equally split between call index values 2 and 3 on tracks 2 and 8 (Figures 2.1b and 2.1h). For 11 of the 12 tracks, call index values assigned by respondents differed from those predetermined by the authors ($P < 0.05$). Combining call index values 2 and 3 only improved the respondents' abundance estimation on one track. In most cases, the deviation from the expected call index values was due to either not recording a species as present (assigning a call index of 0) or discrepancies among volunteers in abundance estimation when a species was recorded as present (Figure 1a-l). Track 8 was an exact repeat of track 2, and 75.2% of respondents identified the same species in both tracks. However, of those respondents that identified the same species in both tracks 2 and 8, only 43.8% of them assigned the same call indices to those species in both tracks. In 3 x 3 contingency table analyses of volunteer experience level (novice, intermediate, or expert) and abundance estimation (correct, over- or underestimation) for each species, only two tests produced significant associations (6.7% of comparisons). Novice observers tended to overestimate northern leopard frogs on track 9 while intermediate and expert observers underestimated calling intensity ($\chi 2_4 = 51.0047$, $P < 0.001$), and correct index assignment was positively associated with observer experience for mink frogs on track 12 ($\chi^2_4 = 10.8867$, $P = 0.0279$).

Discussion

The MFTS was modified from protocols originally developed by the WDNR and NAAMP. NAAMP supplies randomly generated route maps to interested volunteers, and the volunteer then chooses sites based on an equidistant or stratified-by-habitat method (Weir and Mossman, in press). The MFTS instructs volunteers to select the area where they first establish a route, then choose sites without regard to anuran presence (Sargent 2000). While there are likely some volunteers who are knowledgeable about wetland locations and who have paid attention to the frogs calling at these wetlands before involvement in the MFTS, most volunteers have no prior experience with the wetlands or the anurans in an area before establishing a survey route (L.G. Sargent, personal communication). As such, sites are chosen haphazardly, only omitting areas that are "too dangerous or too noisy to hear" calling frogs. In addition, the ability to survey a route near an observer's home significantly increases the likelihood of data submission and volunteer retention. Furthermore, the longevity and the large number of routes established for the MFTS dilutes any bias site selection may inherently introduce. The MFTS, NAAMP, and other large-scale amphibian monitoring programs are intended to provide a meaningful and relatively inexpensive method to track changes in distribution and abundance of species with applicability at a variety of scales. Volunteer observers are an integral part of these goals.

The volunteers participating in the MFTS were able to correctly identify Michigan's frogs and toads by their distinctive breeding calls relatively consistently. All species were correctly identified by $\geq$ 60% of respondents, and all but four species were correctly identified by more than 80% of the respondents. Species that were missed or misidentified were most likely due to confusion with other species with similar calls (e.g., northern leopard frogs and pickerel frogs); inability to determine spatial location of call from CD recording and whether that species was present within the wetland site or farther away (e.g., gray treefrogs in tracks 2 and 8, spring peepers in track 7); inability to hear less conspicuous calls masked by more prominent species (e.g., western chorus frogs, *Pseudacris triseriata*, calling in the presence of a full chorus of spring peepers); or unfamiliarity with species not present in volunteers' survey areas (e.g., mink frogs, Fowler's toads, Blanchard's cricket frogs). In general, we view our results as positive affirmation of the data quality of the MFTS; however, there are several concerns that we will address in future analyses and protocol revisions. Additionally, just over half of the active volunteers in this study returned questionnaires, potentially limiting our conclusions and recommendations to the most conscientious observers.

The cases of mistaken species identification probably represent a worst-case scenario. The use of the CD recording has obvious limiting factors that need to be considered when comparing this study with field investigations. The volunteers in this study were not given any background information about the CD recordings. Had that information been available (i.e., date, geographic location, habitat type), identification problems may have largely been avoided. Even so, results indicate the need to review training materials to decrease misidentifications. Many commonly misidentified species pairs do not breed at the same time (e.g., mink frogs and wood frogs) or have differences in habitat preferences (e.g., leopard frogs and pickerel frogs). Ensuring that volunteers know the basic biology of each species in addition to being trained to recognize distinctive breeding calls could greatly improve data accuracy. The relatively low proportion of respondents who correctly identified Fowler's toads is also a concern; it appears that many observers are not trained to document potential range expansions or isolated populations. Additionally, the CD was produced from field recordings, and truth is not positively known for the recordings. The authors and additional experts independently and unanimously determined species presence and their call index values, but volunteer responses are being compared to authors' identifications and index value assignments and not to true population sizes.

The breeding habits and call characteristics may also affect the probability of detection of a species. Some species simply have a boisterous, unmistakable call (e.g., spring peepers) that is much easier to distinguish than a call that is much more subtle and lower in volume (e.g., northern leopard frogs). Bishop et al. (1997) attributed the paucity of records for breeding leopard frogs in Ontario to its subtle call and lack of concentrated choruses. Our results also indicate that some species may be missed as a result of not being heard over the din of louder species in greater concentrations. Western chorus frogs frequently call at the same time and location as spring peepers, but it can be hard to discern the calls of western chorus frogs within the deafening chorus of spring peepers.

Volunteers spanned a wide range of ages and backgrounds. The mean age was 50.52 yrs., and although some hearing loss is expected with age, the 13 species of Michigan frogs typically call between 300 – 3200 Hz (T. O. Matson, Cleveland Museum of Natural History, personal communication), well within the normal range of human acoustical sensitivity. Detection of frog calls also depends on volume, and 95% of men aged 50.4 (average age of men in this study) can detect 250 Hz at 11.78 dB, and 3000 Hz at 25.22 dB (comparable values for women aged 50.6, average in this study, are 10.73 and 18.76 dB for 250 and 3000 Hz, respectively) (G. A. Flamme, University of Iowa, personal communication). The volume at which a frog calls and the distance between it and the observer are very important factors, as well as additional external noise (e.g., vehicle traffic). We acknowledge that the average age of the MFTS volunteer is middle-aged, and there may be issues related to hearing loss. We will continue to investigate the potential influences of age-related hearing loss on our data quality.

Evaluation of volunteer collected data for other amphibian monitoring programs has indicated that inter-observer agreement on presence and abundance estimation is generally high, but experience also plays a role in data quality (Shirose et al. 1997, Hemesath 1998). Contrary to results from other regional amphibian monitoring programs using call surveys, observer experience played only a minor role in the MFTS. Perhaps, this reflects the fact that our volunteers had an average of 24 years of wildlife experience and had participated in the MFTS for more than 4 years of participation (Table 1). Observer experience level was not a significant influence in either the identification or abundance estimation for any Michigan anuran. Other investigators have found that inter-observer agreement on species presence was very high and not influenced by experience (>96% agreement regardless of experience level, Shirose et al. 1997), but agreement on calling intensity varied with experience level (47-83% in Ontario, Shirose et al. 1997; 56-83% in Iowa, Hemesath 1998). Novice observers tended to underestimate calling intensity relative to experts (Shirose et al. 1997). Similarly, for the North American Breeding Bird Survey (BBS), observer differences were related to experience such that observer quality increased over time (Sauer et al. 1994). First-time BBS observers tended to underestimate species and individuals, and population analyses of BBS data include observers as covariates in order to avoid confounding observer quality with population trends (Erskine 1978, Kendall et al. 1996). Since experience level of the MFTS volunteers did not influence abundance estimation, observer experience level should not affect analyses of changes in abundance over time.

Although observer experience was not an influential factor, there were dramatic differences among volunteers in the assignment of call index values. In many cases, almost the same proportion of survey respondents assigned two different call index values. In general, observers assigned a call index value of 1 with reliability and consistency, but had difficulty distinguishing between call index values 2 and 3. The subjective interpretation of overlapping calls being distinguishable as individuals or not is the difference between call index values 2 and 3. The character of the individual species' calls also influenced observers' ability to assess abundance and assign the correct abundance index. Shirose et al. (1997) also found that inter-observer variation in estimation of calling intensity depended on the species considered. Species with prolonged calls (e.g., American toads, *Bufo americanus*) do not appear to overlap as much as species with shorter calls (e.g., spring peepers). In other states' amphibian monitoring programs, volunteers seemed able to reliably determine the call index of 1, but often had trouble discerning between call indices of 2 and 3 (L.B. Johnson, University of Minnesota, Duluth, personal communication). One solution would be to translate the data into a three-level abundance index: absence (0), low abundance (1), and high abundance (2). In addition to inter-observer differences, we also need to consider intra-observer differences in species detected and call index values assigned. With the duplicate tracks present on the CD, we found that there was relatively low agreement in call index values assigned by the same volunteer. While the combination of call index values 2 and 3 would improve the agreement in abundance estimation, this is a concern that we need to address in our training packet and communications with volunteers.

A related concern is the relationship between the calling index and the actual population size for each species. As a result of the different call characteristics of the 13 species of Michigan anurans (e.g. the long trill of east. American toads compared to the short call of the spring peeper), the same call index value recorded for different species will translate to very different population sizes. The relationship between call counts and population size has been investigated for some species (Shirose et al. 1997), although until empirical calling index – population size relationships can be developed for all species involved, call index values may be best translated into presence/abundance data that can be used to track changes in populations over time (Weir and Mossman, in press).

An inevitable component of a large-scale regional monitoring program is differences among observers. There is a trade-off between the amount and extent of the data and its reliability and consistency. While some monitoring programs have reported significant differences among volunteer observers, in other programs it does not appear to be a major concern (Mossman et al. 1998, Kline 1998). Observer bias is considered minimal in some programs as a result of a combination of their volunteers' experience, scientific evaluation of the data, and number of observations (C. M. Francis and A. Chabot, Long Point Observatory, unpublished report, Mossman et al. 1998, Kline 1998). For amphibian call surveys in Wisconsin, increasing the number of observations (i.e., the number of routes surveyed) reduced variability in the dataset more than increasing volunteer training (Kline 1998). Similarly, power to detect significant population trends in the Marsh Monitoring Project increases as more stations are surveyed (C. M. Francis and A. Chabot, Long Point Observatory, unpublished report). It appears that widespread species that call frequently can be adequately monitored with roadside call surveys; species that call infrequently may require more effort (i.e., more routes surveyed) to track meaningful population trends (Crouch and Paton 2002). Although there were some differences among observers in abundance estimation, we have data from more than 400 survey routes statewide (with 10 wetland sites along each route). With such a great number of sites surveyed each year, we should have the power to track significant population trends over time. However, a formal power analysis should also be conducted.

With respect to the MFTS, we recommend that volunteers refresh their skills prior to each survey season. Being familiar with the basic biology, phenology, range, and habitat requirements of Michigan's frogs and toads would help avoid some simple identification mistakes found in this study. Additionally, NAAMP is currently developing an online frog survey quiz for volunteers. When operational, the MFTS will consider volunteers' quiz scores when determining the inclusion of their data. We also encourage the volunteers to review and adhere to MFTS protocols. There was substantial variability in amount of time spent listening at survey sites. Although most species are heard within the first minute of a survey, and 3 minute stops have been recommended for call surveys (Shirose et al. 1997), volunteers should be strongly encouraged to follow MFTS written protocols to ensure standardization of time spent at stops.

Concerning analyses of sites occupied by each species and changes in occurrence over time, presence is a reliable observation by volunteers, but absence at a site is not guaranteed by undetected calling males. For analyses of abundance trends, we propose combining call index values 2 and 3. While some resolution will be lost by eliminating one abundance category, there is so much variability among observers in assigning call index values 2 and 3 that any apparent difference between the two abundance categories may not be biologically meaningful. We also recommend that verification in the form of a photo, recording, or expert observation be required for rare and hard-to-identify species

(Blanchard's cricket frogs and Cope's gray treefrogs). In addition to these two species, we also encourage verification for pickerel frogs and may make this a requirement in the future. Finally, the training and refresher workshops offered in the past have been very successful and well attended. We recommend that funding and personnel be made available to continue to offer these workshops periodically.

The observer evaluation process presented here is a valuable tool that could be implemented by other regional anuran monitoring programs. One caveat is that similar studies should provide information on time of year and site characteristics with the CD recording. If we had provided that information, the misidentifications may have been reduced. Even so, our results indicate that data from the MFTS can reliably be used to track trends for most species of frogs and toads. Data quality is a major concern in large-scale long-term monitoring programs, and documenting differences among observers is essential for the analysis and interpretation of the data. The detection and abundance estimation of frogs and toads are likely influenced by a variety of factors, and confidence in the data and any resulting trends is greatly improved when the influences of observer bias on the data collection process are understood and documented.

Acknowledgements

C. A. Lepczyk, T. M. Burton, S. K. Hamilton, P. Paton, G. C. White, I. Kiyak, A. Souza, M. J. Sanrcgret, K. B. Joldersma, D. J. Hall, J. Liu, and an anonymous reviewer provided valuable comments on earlier drafts. J. McGrath provided frog call recordings. J. H. Harding and J. McGrath provided expert identifications and abundance estimation for the CD recording. We thank the hundreds of volunteers in the Michigan Frog and Toad

Survey for their continuing efforts. Funding was provided by the MDNR Wildlife Division, Michigan State University chapter of Sigma Xi, and the Ecology, Evolutionary Biology and Behavior graduate program at Michigan State University.

Table 2.1

Demographic characteristics of survey respondents. Means and SE were calculated from all volunteers returning questionnaires, and the sample size for each demographic character (i.e., number of respondents providing answer on questionnaire) is listed in the last column.

Demographic character	Mean	SE	Range	*n*
Involvement with program to date (yrs.)	4.67	0.13	1-6	175
Total anticipated involvement (yrs.)	10.04	0.32	3-30	142
Wildlife experience (yrs.)	24.01	1.28	1-65	168
Age (yrs.)	50.52	0.86	17-81	177

Table 2.2

Proportion of respondents identifying species on each track of the CD recording. Species present on each track are indicated with an asterisk.

Track	Fowler's toad	wood frog	west. chorus frog	spring peeper	north. leopard frog	pickerel frog
1	<0.01	0.16	0.76*	1.0*	0.90*	0.10
2	0.01	0.03	0.03	0.04	0	0
3	<0.01	0	0	<0.01	0	0
4	0.02	<0.01	0.04	0.90*	<0.01	<0.01
5	0	0.87*	0.64*	0.99*	0.56*	0.13
6	0.02	0.04	0.04	0.91*	0.85*	0.17
7	0.60*	0.03	0.13	0.60*	0	<0.01
8	0	0.02	0.03	0.03	0	<0.01
9	<0.01	0.07	0.03	0.80*	0.87*	0.11
10	0.03	0.01	0.10	0.93*	0.22	0.69*
11	0.06	0	0.01	0.08	0	<0.01
12	0.01	0.24	0	<0.01	<0.01	0.02

Table 2.2, Cont'd

Track	east. American toad	gray treefrog	Cope's gray treefrog	Blanchard's cricket frog	mink frog	north. green frog	bullfrog
1	0.02	0.05	<0.01	0.01	0	0.01	0
2	0	0.15[a]*	<0.01	0.85*	0.04	0.99*	0.99*
3	0.99*	0.03	<0.01	0	0	<0.01	0
4	<0.01	0.93*	0.06	0	0	0.99*	0
5	<0.01	0.02	0	0.05	0.09	0.01	0
6	0.99*	0.89*	0.05	0.02	0.04	0.03	0.02
7	0.04	0.56	0.32	0	0	0	<0.01
8	0.01	0.13[a]*	0.03	0.86*	0.06	0.98*	0.98*
9	0.90*	0.02	0	<0.01	0.10	0	0
10	0	0.02	0	0.01	0.04	0.01	0.01
11	<0.01	0.94*	0.87*	0.02	0.01	0	0
12	0	<0.01	<0.01	0.03	0.71*	0.97*	0.04

---

[a] Gray treefrogs may be calling from location outside survey site that cannot be determined from CD recording. This species was omitted from statistical analyses for these tracks.

Table 2.3

Summary of correct identifications and identification errors averaged over all 12 CD tracks (means and SE reported). All means represent proportion of total respondents. Correct identifications indicate volunteers who correctly recorded a species as present when it was calling. Missed identifications indicate volunteers who recorded a species as absent when it was actually present. Incorrect identifications indicate volunteers who recorded a species present when it was absent from the recording. Species with no SE value were present on only one track, precluding estimation of variability.

	Correct		Missed		Incorrect	
Species	Mean	SE	Mean	SE	Mean	SE
Fowler's toad	0.602		0.398		0.015	0.005
wood frog	0.864		0.136		0.055	0.023
west. chorus frog	0.701	0.059	0.299	0.059	0.041	0.013
spring peeper	0.874	0.052	0.126	0.052	0.033	0.013
north. leopard frog	0.795	0.080	0.205	0.080	0.029	0.027
pickerel frog	0.688		0.313		0.051	0.019
east. American toad	0.957	0.031	0.043	0.031	0.010	0.004
gray treefrog	0.917	0.014	0.083	0.014	0.099	0.077
Cope's gray treefrog	0.873		0.127		0.043	0.028
Blanchard's cricket frog	0.858	0.006	0.142	0.006	0.014	0.005
mink frog	0.705		0.295		0.034	0.011
north. green frog	0.984	0.004	0.016	0.004	0.009	0.003
bullfrog	0.981	0.006	0.019	0.006	0.008	0.004
all species combined	0.831	0.034	0.169	0.034	0.034	0.007

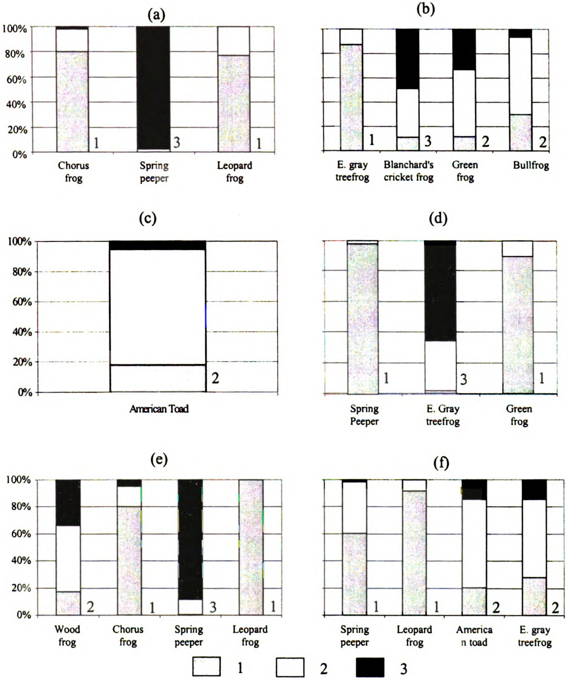
Table 2.4

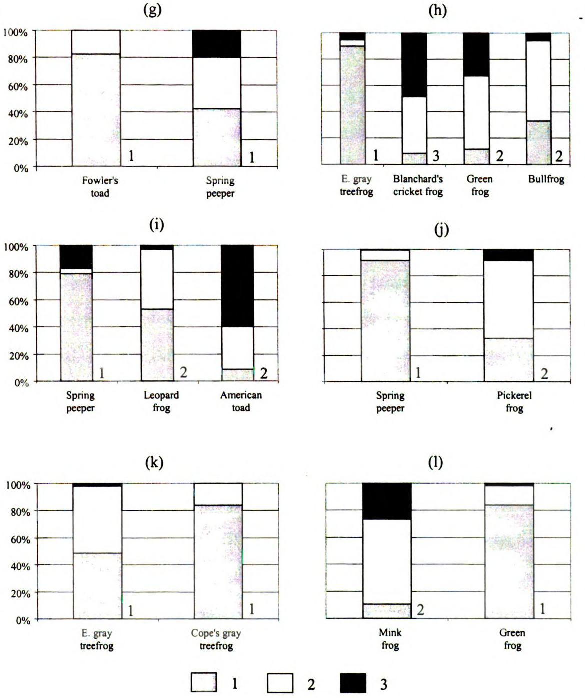
Percentage of respondents living within and outside ranges of the three species with limited distributions within Michigan with correct species identifications. The relationship between living within a limited range and correct identification was tested using contingency table analyses.

Species	Within range	Outside range	χ^2_1	*P* value
mink frog	75.0%	69.9%	0.2216	0.638
Fowler's toad	63.8%	59.2%	0.3265	0.568
Blanchard's cricket frog (track 2)	89.5%	78.6%	3.5559	0.059
Blanchard's cricket frog (track 8)	87.2%	84.3%	0.2711	0.603

Figure 2.1

Call indices assigned by respondents for each CD track. Lightly shaded bars indicate call index 1, open bars indicate call index 2, and black bars indicate call index 3. Y-axis (percentage of respondents) is the same for all figures. Correct call index values are given at the base to the right of each bar. (a) Track 1, (b) Track 2, (c) Track 3, (d) Track 4, (e) Track 5, (f) Track 6, (g) Track 7, (h) Track 8, (i) Track 9, (j) Track 10, (k) Track 11, (l) Track 12.


(a)
100%
80%
60%
40%
20%
0%
Chorus frog
1
Spring peeper
3
Leopard frog
1
(b)
E. gray treefrog
1
Blanchard's cricket frog
3
Green frog
2
Bullfrog
2
(c)
American Toad
2
(d)
Spring Peeper
1
E. Gray treefrog
3
Green frog
1
(e)
Wood frog
2
Chorus frog
1
Spring peeper
3
Leopard frog
1
(f)
Spring peeper
1
Leopard frog
1
America n toad
2
E. gray treefrog
2
1
2
3


(g)
100%
80%
60%
40%
20%
0%
1
1
Fowler's toad
Spring peeper
(h)
1
3
2
2
E. gray treefrog
Blanchard's cricket frog
Green frog
Bullfrog
(i)
100%
80%
60%
40%
20%
0%
1
2
2
Spring peeper
Leopard frog
American toad
(j)
1
2
Spring peeper
Pickerel frog
(k)
100%
80%
60%
40%
20%
0%
1
1
E. gray treefrog
Cope's gray treefrog
(l)
2
1
Mink frog
Green frog
☐ 1
☐ 2
■ 3

Chapter Three

The Influence of Landscape Characteristics on the Abundance and Distribution of Frogs and Toads in Southern Michigan

Abstract

A variety of environmental factors operating at multiple spatial scales are likely responsible for shaping anuran populations and communities. Increased interest in and debate concerning the causes of global amphibian declines is driving research with respect to factors that govern amphibian population dynamics. In this study, land cover variables adjacent to and in the landscape surrounding breeding sites within potential anuran dispersal distances were examined to assess their influence on anuran presence, abundance, and site species richness in southern Michigan using GIS analyses of call survey and land cover data. Short-term temporal patterns (1996-2002) of species richness and individual species' occurrence and abundance at breeding sites in differing landscape contexts were also assessed. Species richness at survey sites was positively related to open land and nonforested wetlands, but lacked the negative associations with urban land and roads and positive associations with forest cover typically reported in the literature. Species richness declined slightly at survey sites in natural contexts, but showed no significant temporal patterns in anthropogenically influenced landscapes. Anuran presence and abundance were influenced by many landscape variables that were generally related to their habitat preferences. The presence and/or abundance of most species was negatively influenced by land cover types representing habitat alteration or loss and positively influenced by land cover types representing potential habitat in the landscape surrounding breeding sites. Species showed few consistent patterns of presence and/or abundance in breeding sites of differing landscape contexts, although *Acris crepitans blanchardi* declined in abundance in anthropogenic context breeding sites and increased in calling intensity in natural context breeding sites. Anuran diversity in southern Michigan appears to be enhanced by a mosaic of land use types surrounding their wetland breeding habitats. The associations I found between anuran occurrence or abundance and land cover types at the landscape level provide valuable information for managing and conserving habitats for these organisms in areas where populations may be low or in decline.

Introduction

Amphibians are an important component of forested ecosystems, comprising a major portion of vertebrate biomass in these systems (Burton and Likens 1975). They are also potentially sensitive environmental indicators due to use of multiple habitats throughout their life cycles, permeable skin, sensitivity to water chemistry during the larval stage, trophic linkages, and metapopulation structure around discrete wetland breeding habitats (Stebbins and Cohen 1995, Bowers et al. 1998, U.S. EPA 2002). As a result of amphibians' environmental sensitivity the herpetological community has been focused on understanding recent population declines around the world (Houlahan et al. 2000). A host of factors has been identified as probable causes contributing to the declines, including ultraviolet radiation (e.g., Blaustein et al. 1997, Licht and Grant 1997), predation (e.g., Fisher and Shaffer 1996, Kiesecker and Blaustein 1997), habitat modification (i.e., loss, alteration, and fragmentation) (Johnson 1992, Hecnar and M'Closkey 1996), chemical contaminants (e.g., Freda et al. 1991, Carey and Bryant

1995, Horne and Dunson 1995), disease (e.g. Berger et al. 1998, Muths et al. 2003), and climate change (e.g., Carey and Alexander 2003). Synergistic interactions among combinations of these factors further complicate the issue of declining amphibian populations (Kiesecker et al. 2001).

Although the causes of these amphibian declines have not been unambiguously determined, habitat modification, including habitat loss and fragmentation, is widely considered to be the most important factor affecting amphibian distribution and abundance (Blaustein et al. 1994a, Pechmann and Wilbur 1994). Indeed, Fahrig (1997) has suggested that the effects of habitat loss far outweigh fragmentation in determining species' risk of extinction. Given the common requirement among amphibians for more than one habitat during different life history stages or seasonally for adults, habitat loss in multiple ecosystem types is an especially dire concern for these organisms (Pope et al. 2000).

Most amphibians are dependent on wetlands ecosystems for at least part of their life cycle, and many species are wetland-associated throughout their entire lives. Wetlands were historically distributed discontinuously across the landscape (Hollands 1987, Winter 1988); amphibian populations are likewise patchy and fit well within the framework of metapopulation dynamics (e.g., Sjögren 1991, Bradford et al. 1993, Alford and Richards 1999). Wetland habitats in the Midwestern United States have suffered losses in excess of 75% for areas dominated by agricultural, industrial, and urbanized activity (Detenbeck et al. 1999). The loss of wetlands increases isolation and reduces the probability of movement among wetland habitats, which can subsequently interfere with metapopulation dynamics characteristic of many species (Gibbs 1993, Sjögren-Gulve 1994, Semlitsch and Bodie 1998).

Aside from habitat loss, landscape-level factors are very important in structuring amphibian communities. The best documented effects of landscape variables on amphibian distribution and abundance are associated with wetland isolation, land cover types and landscape context. Fewer anuran species are likely to be present in isolated wetlands, due to reduced colonization when potential breeding sites lie outside the maximum migration distance (Gibbs 1993, Vos and Stumpel 1995, Findlay and Houlahan 1997, Lehtinen et al. 1999). Altered land uses (i.e., agriculture, urban) also negatively affect anuran abundance by reducing habitat availability and suitability (Brodman and Kilmurry 1998, Knutson et al. 1999). Amphibian distribution and abundance are dependent on landscape connectivity and available forested habitat surrounding wetland breeding sites (Findlay and Houlahan 1997, Hecnar and M'Closkey 1998, Lehtinen et al. 1999, Knutson et al. 1999, 2000).

Road networks are another feature of human-dominated landscapes with profound effects on amphibian populations. Roads are both a structuring force on the landscape and a significant barrier to anurans (Forman and Alexander 1998, Trombulak and Frissell 2000). For example, road mortality poses a significant threat to anurans migrating to and from breeding sites, and amphibian abundance is reduced in areas with high road densities and/or traffic volume (Reh and Seitz 1990, Fahrig et al. 1995, Ashley and Robinson 1996, Vos and Chardon 1998, Carr and Fahrig 2001).

Evaluation of the influence of landscape characteristics on anuran communities is vital for management and conservation of these sensitive species. The documented

importance of landscape characteristics on amphibian distribution and abundance in other midwestern regions (e.g., Minnesota, Lehtinen et al. 1999; Wisconsin and Iowa, Knutson et al. 1999, 2000), suggested the need to investigate landscape influences on frogs and toads in southern Michigan. The objective of this study was to determine the influence of surrounding landscape on amphibian presence, abundance, and species richness by investigating the importance of different land use types and roads on amphibian breeding sites surveyed annually in the Michigan Frog and Toad Survey (MFTS). I evaluated the following hypotheses: (1) anuran species associated with forested areas for at least a portion of their life cycles should be sensitive to the total area of forest surrounding breeding sites, compared with species that can utilize a wider variety of habitat types; (2) since all Michigan anurans are dependent on wetland breeding sites for annual reproductive events, they should be sensitive to the total area or proportional coverage of aquatic habitats (forested and nonforested wetlands, water) surrounding breeding sites; and (3) vagile species that are potentially capable of moving long distances through different habitat types should be less sensitive to altered land cover types than species that have limited movement capabilities and are dependent upon specific habitat types in a much smaller area.

Methods and Materials

Michigan Frog and Toad Survey

In 1996, the Michigan Department of Natural Resources (MDNR) established an annual frog and toad survey that uses a network of volunteer observers throughout the state to monitor breeding anuran populations (Sargent 2000). Twelve species of anurans are found in southern Michigan (Table 3.1). The MFTS currently has annual data for approximately 350 routes surveyed statewide since 1996 in Michigan (Figure 3.1). Detailed protocols for the MFTS can be found in Sargent (2000), but are summarized below (see also Chapter One). Each route consists of 10 wetland sites selected by volunteers; these sites are separated by at least 400 m such that the origin of calls can be unambiguously determined for each site. The volunteers then survey their routes three times each spring and early summer (according to minimum temperature guidelines and with at least two weeks between successive survey dates) and record the identity of each species and an index of calling intensity. Volunteers are instructed to conduct surveys after dark, beginning one-half hour after sunset and finishing before midnight, and under favorable conditions of appropriate temperatures and little or no wind. Intensity of calling males is rated 0 through 3, with 0 = no individuals calling, 1 = few individuals with non-overlapping calls (1-5 individuals), 2 = distinguishable individual calls that overlap (6-12 individuals), and 3 = full chorus with indistinguishable individual calls (13+ individuals).

The call index data were combined for the two gray treefrog species (*Hyla versicolor* and *H. chrysocelis*) prior to analyses. The calls of these two morphologically identical species are difficult to distinguish, and temperature can affect the pulse rate and duration of their calls, making them very difficult to identify in single species choruses (Harding 1997). Verification for *Hyla chrysoscelis* in the form of recording or expert opinion became a requirement in 1998, but prior to that, the identities of the two treefrog species were not formally determined. Therefore, some records for *H. chrysoscelis* prior to 1998 may represent *H. versicolor* and vice versa.

In 2003, there were 255 active MFTS routes in southern Michigan (L.G. Sargent, MDNR, pers. comm.; Figure 3.1). Data were included for a species if surveys were complete on an annual basis (i.e., completed all three survey runs during appropriate times and weather conditions each year) and data had been submitted for that route at least three years during the entire MFTS period (1996-2002). There were 1055 survey sites representing 127 routes in southern Michigan that satisfied the selection criteria. All sites were included for those species with distributions throughout southern Michigan, and a subset was included if species had a restricted distribution (*Bufo fowleri;* 651 sites representing 74 routes). The maximum call index value assigned to a species in any of the surveyed years was defined as the abundance index of that species at that site. This value represents the highest abundance of a species during the survey period and provides a good estimate of the wetland breeding site's potential given the highly variable nature of amphibian population dynamics over time (Pechmann and Wilbur 1994, Semlitsch et al. 1996).

Landscape Variables

MFTS listening points were located on digital USGS 7.5 minute quadrangle maps, and coordinates were displayed in ArcGIS (ArcMap 8.2, ESRI, Redlands, CA). Land cover data were obtained from the Michigan Department of Natural Resources (MDNR) and the Michigan Geographic Data Library. Land cover data for the southern lower peninsula were derived from classification of Landsat Thematic Mapper (TM; 30 m resolution) images from 1997-2000. Land cover classifications of the data were simplified to the following seven categories that generally correspond to the major classes on the statewide land cover map used by the MDNR: (1) urban (airports, parking lots, low to high intensity urban), (2) agriculture (non-vegetated farmland, row crops, forage crops, orchards, vineyards, and nurseries), (3) open land (parks, golf courses, herbaceous open land, upland shrubs, low density trees), (4) forest (upland deciduous and coniferous forests), (5) forested wetlands (lowland forests with >25% tree cover), (6) nonforested wetlands (<25% tree cover including floating aquatic plants, emergent wetlands, and lowland shrubs, and (7) open water (permanent ponds and lakes). The road network coverage was obtained from the Michigan Geographic Data Library. This data set is part of the Michigan Geographic Framework, which serves as the digital base map for State of Michigan government agencies. The geographic framework was created from multiple data sources from the time period 1997-2002.

Two buffers were created around each survey site to characterize the area surrounding breeding sites and quantify the landscape variables. The center of each buffer was the MFTS observer's listening point. A buffer of 100 m was determined to be the smallest size to characterize the land use directly adjacent to the survey point given the resolution of the land cover data, and a buffer of 1000 m was used to determine the potential influence of landscape characteristics on anuran presence, abundance, and species richness. This distance also represents the dispersal range of many anuran species (Merrell 1977, Berven and Grudzien 1990, Sinsch 1990, Stebbins and Cohen 1995) and has been found to be an optimal distance for landscape characterization in other amphibian landscape studies (e.g., Vos and Stumpel 1995, Knutson et al. 1999, Pope et al. 2000, Guerry and Hunter 2002). For each land cover category, total area (m^2) of each land cover type surrounding the anuran survey site was calculated at each scale (100 m and 1000 m). Total road length was also calculated at each scale. There was a total of seven land cover variables (total area of each land cover type within buffer) and one road variable (total road length within buffer) at each scale.

Variables describing the area of land cover types and road length were chosen over other landscape indices for several reasons. Other studies have found area of land cover types to be most strongly related to amphibian variables (e.g., Vos and Chardon 1998, Lehtinen et al. 1999, Knutson et al. 1999). The nature of both the land cover data (original coverages were raster and converted to polygon) and MFTS data (listening points were along roadsides and did not necessarily plot within a wetland on the land cover map) also led to the selection of the suite of variables in this study. The metrics chosen in this study were intended to characterize the potential influences of different land cover types and roads on anuran dependent variables.

Landscape Context and Temporal Patterns

MFTS survey sites were classified into four landscape contexts based on the proportional coverage of each land cover type in a 1000 m radius surrounding the breeding site. Each landscape context consisted of sites that were primarily (>50% of surrounding land cover) urban, agricultural, forested, or wetlands (both forested and nonforested wetlands combined). The other land cover types (open land and water) did not comprise the majority of total land area surrounding any of the breeding sites. Short-term temporal patterns (1996-2002) of species richness were evaluated in these four landscape contexts, as well as in a broader anthropogenically influenced landscape context (urban and agriculture combined) and natural landscape context (open land, forest, wetlands, and open water combined). Individual species occurred at too few sites in the four landscape context categories (urban, agriculture, forest, and wetlands), and temporal patterns of occurrence and abundance were assessed in anthropogenically influenced vs. natural landscape contexts (Lepczyk 2002). Occurrence in anthropogenically influenced and natural landscape contexts was assessed by evaluating temporal changes in the proportion of sites sampled annually occupied by each species from 1996-2002. Calling intensity of breeding males was used to assess abundance; patterns in mean annual call index values were used to evaluate temporal patterns in abundance in each landscape context.

Statistical Analyses

After examination of descriptive statistics and normal probability plots for original variables and potential data transformations, all landscape variables were log (x + 0.5) transformed prior to statistical analyses. Principal components analysis (PCA) was used to summarize the variation in landscape characteristics separately at each scale (Morrison 1990). The resulting principal components (PCs) represented a reduced number of independent variables that were then used to investigate relationships between landscape variables and anuran presence, abundance, and species richness. Only the PCs that explained a significant amount of variation in the original dataset were retained for further analyses; total variation explained at each of the spatial scales was $\geq$85%. All data analyses described below were carried out using both the original (log-transformed) landscape variables and PCs at each buffer scale to determine which variables explained a higher proportion of total variation in the models, and would thus have the highest potential for application to management and conservation strategies.

Multiple regression analyses were used to examine how individual landscape variables and principal components were associated with anuran abundance and species richness (Jongman et al. 1995, Lehtinen et al. 1999, Knutson et al. 1999, 2000). Logistic regression was used to determine the explanatory power of landscape variables and principal components on species presence (Jongman et al. 1995, Vos and Chardon 1998, Guerry and Hunter 2002). Both original (log-transformed) land cover variables and principal components were used to construct regression models to identify which variables (land cover or principal components) were most influential and practical for future management and conservation applications. Temporal patterns of species richness and individual species' occurrence and abundance were evaluated using simple linear regression techniques. All data analyses were performed using SYSTAT (version 8.0, SPSS, Inc. 1998) and SAS (release 8.02, SAS Institute 2002).

Results

Three land cover types dominated the landscape surrounding MFTS sites: agriculture, forest, and nonforested wetlands. At both buffer scales, these three variables comprised >62% of the total buffer area (Table 3.2). These three land cover types had the greatest total area compared to all other land cover types, although their rankings differed slightly between the two buffer scales (Table 3.2). Within 100 m adjacent to the survey site, forest was the dominant land cover (24.2%), followed by agriculture (20.5%) and nonforested wetlands (17.3%) (Table 3.2). In the landscape up to 1000 m from the survey site, agriculture was the dominant land cover type (32.2%), followed by forest (26.3%) and nonforested wetlands (11.4%) (Table 3.2). At both scales, water was the least abundant land cover type, covering < 3% of the buffer area (Table 3.2). There was an average of 211.42 m (std. error = 2.19 m) of roads within 100 m of survey sites, and 7689.12 m (std. error = 157.58 m) of roads within 1000 m (Table 3.2).

Principal Components Analysis

Principal components analyses of landscape variables at the 100 m scale yielded a reduced set of four independent variables that explained approximately 85% of the total variation in the original data set (Table 3.3). Examination of eigenvalue plots from the retained PCs provided insights into the original variables that were highly influential in the dataset and contributed to the ordination of the PCA (Figure 3.2, Table 3.3). The first PC represented a contrast between agricultural and both forested and nonforested wetland sites. The second PC represented a contrast between open or forested sites and those in agricultural or wetlands context. The third PC represented a weighted average of all variables. However, three variables (agriculture, open, and forest) were most influential in the ordination of the third PC, and two variables (roads and urban) contributed very little. The area of open water surrounding survey sites dominated the fourth PC.

At the 1000 m buffer scale, PCA produced two PCs that accounted for >93% of the total variation (Table 3.4). The first PC was heavily dominated by water, and the second PC was heavily dominated by agriculture (Table 3.4, Figure 3.3). All other variables contributed very little to the ordination.

Species Presence

Logistic regression analyses at both spatial scales revealed several landscape variables that significantly influenced species presence at survey sites. Immediately surrounding survey sites (100 m buffer scale), the variables that were most often significantly related to species' abundances and site species richness were agriculture, water, urban, and nonforested wetlands (Table 3.5). Agricultural land cover was most frequently associated with anuran occurrences, as indicated by significant relationships in 8 of the 11 cases (Table 3.5). These relationships were evenly split between both positive and negative. The second most frequent land cover association was found between water and anuran occurrence, with significant relationships seen for 7 of 11 species (Table 3.5). These relationships were also approximately evenly split between negative (4 species) and positive (3 species) associations (Table 3.5). Urban land was significantly associated with 6 of 11 species (Table 3.5). All but one species was significantly negatively associated with urban land (Table 3.5). Six species were also significantly associated with the area of nonforested wetlands (Table 3.5). These relationships were generally positive associations, although two species were negatively related to area of nonforested wetlands adjacent to survey sites (Table 3.5). All other land cover variables were significantly associated with fewer than half of the species in the study area.

At the 100 m scale, principal components 1 and 4 each were significantly associated with the occurrence of three species, while PC 2 was significantly related to the occurrence of four species (Table 3.6). PC 1, a contrast between agricultural and wetland sites, was significantly positively related to the occurrence of *R. clamitans* and *R. catesbeiana*, and was negatively associated with *B. americanus* presence (Table 3.6). PC 2, a contrast between open or forested sites and agricultural or wetland sites, was consistently negatively related to the presence of *P. triseriata, R. pipiens, R. palustris,* and *H. versicolor/chrysoscelis* (Table 3.6). PC 3 was a weighted average of all land cover types, but was not significantly related to any species' presence. PC 4, area of water surrounding survey sites, was negatively related to the occurrence of *R. sylvatica* and *P. triseriata,* but positively associated with the presence of *A. c. blanchardi* (Table 3.6). Neither *P. crucifer* nor *B. fowleri* occurrence was significantly associated with any of the principal components.

At the broader landscape scale (1000 m radius around survey site), several variables were significantly related to the occurrence of anurans. Urban land was generally significantly negatively related to the presence of anurans (*R. sylvatica, P. crucifer, R. pipiens, B. americanus,* and *A. c. blanchardi*), but positively associated with the occurrence of *R. catesbeiana* (Table 3.7). Forest cover in the surrounding landscape was generally negatively related to the presence of anurans (*R. sylvatica, P. triseriata, R. pipiens, B. fowleri,* and *B. americanus*), but was positively related to the presence of *P. crucifer* and *R. catesbeiana* (Table 3.7). Open land was consistently positively related to the occurrence of *R. sylvatica, P. triseriata, R. pipiens, B. americanus, H. versicolor /chrysoscelis,* and *R. catesbeiana* (Table 3.7). Although total road length was only significantly associated with the occurrence of two species (*P. triseriata* and *H. versicolor/chrysoscelis),* both relationships were negative (Table 3.7). Forested and nonforested wetlands each predicted the occurrence of five species, but the relationships were generally negative although not consistent among all species (Table 3.7). Similarly, water in the surrounding landscape was significantly associated with the occurrence of four species; two species had positive relationships (*R. pipiens* and *R. catesbeiana)* and two had negative relationships (*A. c. blanchardi* and *R. clamitans*) (Table 3.7). Agriculture was significantly negatively associated with the occurrence of *R. catesbeiana* (Table 3.7).

Principal components were significantly associated with the occurrence of just over half of the species present in the study area at the 1000 m buffer scale. The occurrences of five species (*P. crucifer, R. palustris, A. c. blanchardi, R. clamitans,* and *R. catesbeiana)* were not significantly related to any of the PCs (Table 3.8). PC 1, strongly dominated by water, predicted the occurrence of five species; *B. americanus* had a positive relationship while *R. sylvatica, P. triseriata, R. pipiens,* and *H. versicolor/ chrysoscelis* were all negative (Table 3.8). PC 2, strongly dominated by agriculture, was significantly positively related to the occurrence of *R. sylvatica* and *B. fowleri* (Table 3.8).

Species Abundance

Multiple regression models fit the data relatively poorly, explaining less than 10% of the variation in the data accounted for by landscape variables at either spatial scale (Tables 3.9 – 3.12). Regression models built with the original variables explained slightly more variance than those using principal components at either spatial scale.

Directly surrounding survey sites, urban land was significantly negatively related to four species' abundance (*R. sylvatica, R. pipiens, H. versicolor/chrysoscelis,* and *R. clamitans;* Table 3.9). Nonforested wetlands were also significantly positively related to three species' abundance (*R. pipiens, R. clamitans,* and *R. catesbeiana*) as well as site species richness (Table 3.9). Agriculture was a significant factor in the regression models for five species' abundance and overall species richness; however, the direction and magnitude of the trends were not consistent among all dependent variables (Table 3.9). Agriculture was negatively associated with *B. fowleri* abundance, and positively associated with species richness and the abundances of *R. sylvatica, P. triseriata, R. pipiens,* and *H. versicolor/ chrysoscelis.*

Multiple regression models using PCs yielded similar results to those presented above. Six species' abundances were significantly related to PC 4; however, the direction and magnitude of these relationships were also not consistent among species (Table 3.10). *Bufo americanus, A. c. blanchardi,* and *R. catesbeiana* were positively associated with PC 4 (area of open water surrounding survey sites), while *R. sylvatica, P. triseriata,* and *H. versicolor/chrysoscelis* were negatively associated with that PC. The fourth PC also accounted for the least total variation in the dataset (< 9%, Table 3.3). PC 1, a contrast between agricultural and wetland sites, was significantly related to four species' abundances; the relationship was positive for three of those species (*P. crucifer, R. clamitans,* and *R. catesbeiana;* Table 3.10). PC 2, a contrast between open or forested sites and agricultural or wetland sites, was significantly negatively related to *R. pipiens* and *R. palustris* abundance and species richness, and positively related to *B. fowleri* abundance (Table 3.10).

At the larger landscape scale (1000 m buffer), the amount of forested wetlands, open land, water, and urban land were the four most consistent influential variables, with significant trends consistently in the same direction with anuran abundance and species richness (Table 3.11). There were also more significant relationships between land cover types and individual species' abundance at the landscape scale (1000 m buffer) compared to the local scale (100 m buffer). Forested wetlands were significantly positively related to four species' abundances (*R. sylvatica, P. triseriata, R. pipiens,* and *B. americanus*), and open land was also significantly positively related to species richness and the abundances of *P. triseriata, R. pipiens,* and *B. americanus* (Table 3.11). The area of open water in the landscape surrounding survey sites was positively related to the abundances of *R. pipiens, B. americanus, R. clamitans,* and *R. catesbeiana* (Table 3.11). Urban land was significantly negatively associated with the abundances of *R. sylvatica, R. pipiens, B. americanus,* and *H. versicolor/chrysoscelis* (Table 3.11). Agriculture was a significant variable in the regression models for six species and species richness, but the direction and magnitude of the trends were not consistent among all dependent variables (Table 3.11). Somewhat surprisingly, species richness and four species' abundances (*R. sylvatica, P. triseriata, P. crucifer,* and *H. versicolor/chrysoscelis)* were significantly positively related to the amount of agricultural land in the 1000 m buffer around the survey site; significant negative relationships were found for the abundances of *R. clamitans* and *R. catesbeiana* (Table 3.11). The remaining landscape variables (roads, forest, and nonforested wetlands) were significantly associated with individual dependent variables, but the direction and magnitude of the trends were not consistent among species (Table 3.11).

Both principal components were significantly related to site species richness and many species' abundances, with the direction of the trends consistent across all significant relationships. PC 1 was significantly negatively associated with the abundances of *R. sylvatica, P. triseriata, P. crucifer, R. pipiens, H. versicolor/ chrysoscelis,* and *R. clamitans,* while PC 2 was significantly positively associated with site species richness and the abundances of *R. sylvatica, P. crucifer, R. pipiens, B. fowleri, R. clamitans,* and *R. catesbeiana* (Table 3.12). However, all of these relationships explained very little of the total variance in the dataset (R^2 range: <0.001 – 0.068; Table 3.12).

Landscape Context and Temporal Patterns

There were no significant temporal patterns in species richness in any of the four landscape contexts (urban, agriculture, forest, or wetlands), however, species richness decreased slightly over the 1996-2002 time interval in survey sites in natural contexts ($R^2 = 0.019$, $P = 0.026$; Table 3.13). At survey sites in anthropogenic contexts, *A. c. blanchardi* declined significantly in site occupancy ($R^2 = 0.667$, $P = 0.025$; Table 3.14, Figure 3.4), while *R. sylvatica, P. crucifer, R. palustris,* and *R. clamitans* showed significant increases in calling intensity over the same time period ($P < 0.05$, Table 3.15). At sites in natural contexts, *R. pipiens* declined in site occupancy ($R^2 = 0.851$, $P = 0.003$; Table 3.14, Figure 3.5). Mean annual call index values for five species showed significant trends over the time period at survey sites in a natural landscape context; four species increased significantly, and *B. americanus* decreased (Table 3.15).

Discussion

Foremost among the findings was that the occurrence and abundance of anurans, as well as site species richness, exhibited significant relationships with land cover types and roads regardless of the methodology used. The principal components and regression analyses provided qualitatively similar results. Regression analyses using the individual landscape variables will be more useful for the development of future predictive models, while PCA was able to reduce the data to a smaller set of independent variables that provided a composite picture of anuran-habitat relationships. The regression models using original landscape variables explained a higher proportion of variance than those using principal components, which was also the case for a similar study of anuran-habitat associations in Wisconsin and Iowa (Knutson et al. 1999). Using both methods provided complementary information for a more comprehensive understanding of anuran-habitat relationships in southern Michigan.

The regression models accounted for only a small proportion of the total variance (<10%). In other similar studies, the proportion of variance explained by landscape-level factors was greater, yet also relatively small ($\leq$ 20% in Knutson et al. 1999, $\leq$ 35% in Bonin et al. 1997 and Hecnar 1997). These studies differed slightly in the methods used to measure anuran abundance, which may have been influential. Knutson et al. (1999) and Bonin et al. (1997) used call index values from regional monitoring programs, as I did in this study. Hecnar (1997) limited his analyses to landscape-level associations with species richness. Previous studies of anuran-land cover associations in southeastern Michigan also yielded weak but significant relationships (K. S. Genet, unpublished data). In that case, the paucity of strong associations was attributed to a relatively small geographic area (seven counties in southeastern Michigan) with less variation in the distribution of land cover types (highly populated and urban developments) than the larger geographic area considered in this study.

Species richness at wetland breeding sites is generally reduced at sites in urban contexts with more roads and where land cover is dominated by urban or other anthropogenically-modified areas (Lehtinen et al. 1999). Conversely, regional forest cover has been found to be a very important explanatory variable for anuran species richness (Hecnar and M'Closkey 1998). In this study, urban area and roads were not significantly associated with species richness, but agriculture and open land were. Many anurans depend on a complex of habitats throughout their life cycles, and open land including both natural and managed recreational areas provides important foraging habitats for many species. The lack of significant relationships between species richness and urban land or roads was surprising; perhaps future examination of additional landscape characteristics related to habitat fragmentation would clarify these relationships. Some species have adapted quite well to altered habitats in urbanized areas (e.g., *R. clamitans*; Harding 1997, Hecnar and M'Closkey 1997b). Forest cover was also not a significant influence at the 1000 m scale, but perhaps this reflects the diverse habitat requirements of southern Michigan anurans that benefit from a variety of habitat types and include species that are not wholly dependent on woodland habitats.

Individual species varied greatly in their response to landscape variables. Although urban land was not significantly associated with species richness at survey sites, it was negatively related to occurrence and/or abundance for nine of the eleven species in the study area. Urbanization negatively influences anurans as a result of the associated land use changes, including loss of naturally vegetated habitats, industrial land uses, fragmentation of formerly continuous populations and/or dispersal corridors, and a broad range of pollutants and contaminants. Urban land was negatively related to anuran presence and abundance in other studies (Knutson et al. 1999, Lehtinen et al. 1999). Roads were also negatively related to four species. Roads reduce habitat connectivity, and reduced anuran presence and/or abundance in urban areas or those with a high density of roads can be attributed to habitat loss, isolation from neighboring habitats, and dispersal barriers (Mader 1984, Fahrig et al. 1995, Findlay and Houlahan 1997, Lehtinen et al. 1999). Roads are significant barriers to dispersal, and juvenile dispersal is among the most important life history movements linking populations in fragmented landscapes (Brown and Kodric-Brown 1977, Berven and Grudzien 1990).

Forests provide important habitat for many species that spend all or part of their nonbreeding season in trees, shrubs, or litter. Positive associations between forest cover and anuran abundance is one of the most consistent landscape scale habitat relationships reported in the literature (e.g., Strijbosch 1980, Laan and Verboom 1990, Bonin et al. 1997, Findlay and Houlahan 1997, Hecnar 1997, Mitchell et al. 1997, Knutson et al. 1999). In southern Michigan, the species that would be expected to be most sensitive to forest cover are those that spend a considerable amount of time in woodland habitats, including *R. sylvatica, P. crucifer,* and *H. versicolor/chrysoscelis* (Harding 1997).

I did not find consistent positive relationships with forest cover for most species in this study. *Pseudacris crucifer* presence was positively influenced by forest cover at the landscape scale, but negatively associated with forest directly surrounding the surveyed breeding sites. This species uses a wide variety of temporary and permanent wetlands for breeding, but disperse to woodlands after the breeding season (Harding 1997). The occurrence of *R. sylvatica,* the species with the strongest expected sensitivity to forest cover, was surprisingly negatively associated with forest cover at the landscape scale and unrelated to forest cover directly surrounding breeding sites. However, this species was positively influenced by forested wetlands, and lowland forests likely provide more valuable habitat for this species than upland forests. I did not differentiate between different types of forest cover in this study (i.e., deciduous vs. coniferous or natural vs. planted/managed), but these variables may be important for some species and have been more thoroughly investigated in northeastern North America (e.g., Waldick et al. 1999). The presence and/or abundance of other species (i.e., *P. triseriata, R. pipiens, B. fowleri, B. americanus,* and *R. clamitans)* were negatively associated with forest cover, which is likely due to their preference for more open or permanently aquatic habitats (Pais et al. 1988, Koloszvary and Swihart 1999).

Many open habitats provide important foraging habitats for anurans, and several species in southern Michigan use open areas for at least part of their life cycles. I found the presence and/or abundance of *R. sylvatica, P. triseriata, P. crucifer, R. pipiens, B. americanus, H. versicolor/chrysoscelis,* and *R. catesbeiana* to be positively associated with open land. Two of these species, *R. pipiens* and *B. americanus,* are considered to be species with open and generalist habitat affinities, respectively (Harding 1997, Hunter et al. 1999, Guerry and Hunter 2002). Although *P. crucifer* is typically most abundant in wooded areas, they also use a wide variety of open habitats during the terrestrial phases of their life cycle (DeGraaf and Rudis 1990). The open land cover type in this study included areas of herbaceous and woody open land, as well as recreational areas that are suitable habitat for these species.

I expected to find negative associations between anuran presence or abundance and agricultural land. Some agricultural land use practices have the potential to impact aquatic habitats (including anuran breeding sites) by altered nutrient regimes, sediment accretion, changes in water temperature and oxygen content, and increases in pollutants (Abramovitz 1996). These types of habitat changes are likely to negatively affect mortality, reproductive success, growth, and behavior of organisms that live in these habitats (Moyle and Leidy 1992, Saunders et al. 2002). More specifically, modern farming practices are associated with habitat loss, drainage of wetlands, conversion of important habitats to intensively managed monocultures of annual crops, soil compaction, and disturbance to anurans that may spend time in underground habitats (Bonin et al. 1997).

Some species were negatively related to agriculture (*B. fowleri, A. c. blanchardi, R. clamitans,* and *R. catesbeiana),* however, other species were either positively related to agriculture or had mixed responses at the two spatial scales (*R. sylvatica, P. triseriata, P. crucifer, R. pipiens, H. versicolor/chrysoscelis).* Although others have found a negative relationship between agriculture and anurans (e.g., Brodman and Kilmurry 1998), Knutson et al. (1999) also failed to find consistent or strong negative associations between anurans and agriculture. Agricultural landscapes often include small remnant forest patches, which may provide refugia for some species. Although intensively managed and annually cultivated row crops are probably inhospitable to most anurans, other types of agriculture (e.g., forage crops) may offer suitable habitat for anurans during some parts of their life cycles. Distinguishing among these different agricultural practices may be useful in evaluating agricultural land impacts on anurans, but frequent crop rotations make this very difficult. The land cover data used in this study are composite images from multiple years, and some agricultural land was likely rotated between forage and row crops.

All species in this study depend on wetlands for breeding and larval development. Therefore, I expected all species to be positively influenced by the water and wetland areas directly adjacent to and in the landscape surrounding breeding sites. Many species rely on temporary wetlands or shallow, vegetated edges of permanent water bodies for reproduction, and the area of open water adjacent to or in the surrounding landscape of survey sites represented a negative influence for most species (including *R. sylvatica, P. triseriata, P. crucifer, R. palustris, H. versicolor/chrysoscelis, A. c. blanchardi,* and *R. clamitans*). Most open water habitats are permanent ponds or lakes, and predatory fish limit the distributions of many anurans to seasonal freshwater habitats with reduced predation pressure (Wellborn et al. 1996, Hecnar and M'Closkey 1997a). *Rana pipiens, B. americanus,* and *R. catesbeiana* were positively influenced by open water areas. *R. pipiens* and *B. americanus* are open or generalist habitat species that benefit from a variety of land cover types, while *R. catesbeiana* is restricted to breeding only in permanent water bodies as a result of the extended larval development period (Harding 1997).

The area of wetlands (forested and/or nonforested) positively influenced the occurrence and/or the abundance of all but four species (*R. palustris, B. fowleri, H. versicolor/chrysoscelis,* and *A. c. blanchardi*). Those species that were unaffected by wetland area (*R. palustris* and *H. versicolor/chrysoscelis)* are likely more sensitive to other landscape factors, perhaps representing important habitats outside the breeding season. Species that were negatively influenced by wetland area (*B. fowleri* and *A. c. blanchardi*) may be less dependent on areas classified as wetlands and able to use a wider variety of land cover types. Another consideration for wetland habitats is their dynamic nature; climate strongly influences depth and duration, and these characteristics are not reflected in the relatively coarse spatial and temporal resolution (multiple seasons and years) of the land cover data. Those species with positive relationships to wetland area were typically associated with the types of wetlands that comprise their characteristic breeding habitats (e.g., *R. sylvatica* was related to forested wetlands, *R. clamitans* was related to nonforested wetlands). The positive influence of wetlands for most species' presence and abundance probably reflects not only requirements for this habitat type for breeding, but also the importance of connectivity among wetland habitats for metapopulation structure (Sjögren 1991, Gibbs 1993, Semlitsch 2000, 2002).

Over the duration of this study (1996-2002), *Acris crepitans blanchardi*, listed as a species of special concern in Michigan, declined significantly in site occupancy in anthropogenically-influenced and marginally declined in natural landscape contexts. Additional detailed studies on this species need to determine if distributional declines are related to habitat or landscape level factors (Lee 1998, Lehtinen 2001). Calling intensity of most species increased significantly both in anthropogenically-influenced and natural landscape contexts. *Rana sylvatica* and *R. clamitans* increased in abundance (assessed by mean annual call index values) in both landscape contexts. Improvements in survey timing and species detection by volunteer observers probably account for at least a portion of this trend, particularly for *R. sylvatica.*

Anurans in southern Michigan appear to benefit from a mosaic of land use types surrounding their wetland breeding habitats. Some land uses that were hypothesized to be negatively associated with anuran communities may instead provide suitable habitat. As discussed above, some types of agricultural land may provide foraging habitat and not impede movements between other habitat patches. Similarly, low intensity urban areas may also provide suitable habitat for some species, as many areas incorporate small wetlands, constructed ponds, and intermittent woodlots into urban planning. For example, *R. clamitans* has been very successful at colonizing new ponds, including constructed ponds in residential areas (Hecnar and M'Closkey 1997b).

Anurans respond to environmental factors at multiple spatial scales, including both landscape (as investigated here) and within-habitat characteristics. Anuran communities are influenced by habitat factors that determine success and fitness at the population level and landscape factors that determine habitat suitability and connectivity (Lehtinen et al. 1999). Although landscape variables have been shown in other studies to be better predictors of species occurrence than pond water chemistry (Beebee 1985), landscape variables alone have explained $\leq 35\%$ of the variance in other studies (Bonin et al. 1997, Hecnar 1997, Knutson et al. 1999). A combination of local (i.e., habitat) and regional (i.e., landscape) variables best accounted for patterns of species richness in Ontario landscapes (Hecnar and M'Closkey 1998). The potential contributions of many factors to the abundance and distribution of anurans at both local habitat and regional landscape scales indicate the importance of examining variables at multiple spatial scales to understand the factors important in structuring anuran communities.

In this study, the relatively small proportion of total variance explained by the significant relationships is an important limitation of these results. Studies such as this may be limited both by the data collection methods (multiple volunteer observers, nonrandomly selected survey sites, and categorical call index values) and insufficient power to detect significant associations with the statistical methods used (van Dorp and Opdam 1987, Lehtinen et al. 1999). The study sites represent listening points for the MFTS, and these roadside locations may not be precisely located within the breeding pond from which anurans are calling. Some of the survey sites may also be from very small wetlands. While these small wetlands are important habitats for anurans (e.g., Gibbs 1993, Semlitsch and Bodie 1998, Snodgrass et al. 2000), they may be too small to be represented in the land cover data, given its resolution. An additional consideration in the models developed to predict species occurrence is an inherent limitation of the call survey data from the MFTS: while a species documented as calling definitely represents presence at a survey site, species not documented as calling remain undetected as they may be present but unheard by the volunteer observer(s). As a consequence of the limitations of this study, the results should perhaps be viewed as exploratory, and refinement of sampling methods (e.g., intensive quantitative sampling of populations at individual breeding sites) may improve the predictive power of subsequent models. However, data such as these could possibly be used to develop spatial models (e.g., Halley et al. 1996) that can be used to predict the persistence of anuran populations at the landscape level, as long as the limitations of call surveys and inherent low statistical power are addressed.

The associations I found between anuran occurrence or abundance and land cover types at the landscape level provide valuable information for managing and conserving habitats for these organisms in areas where populations may be low or in decline. Population trends determined from monitoring programs (see Chapter One) need to be combined with results such as these to achieve a more comprehensive understanding of anuran-habitat associations. Anuran presence and abundance in southern Michigan are associated with land cover that reflects habitat availability and suitability in this region. Future research should incorporate anuran-habitat associations such as these into the development of practical management and conservation strategies.

Acknowledgements

Land cover data were provided by the MDNR, and C.R. Steen facilitated the conversion and transfer of this data. T.M. Burton, S.K. Hamilton, D.J. Hall, J. Liu, C.A. Lepczyk, and W. Gordon provided valuable editorial comments. Support for this research was provided by the Michigan Coastal Management Program of the Michigan Department of Environmental Quality, National Oceanic and Atmospheric Administration, U.S. Department of Commerce, Geological and Land Management Division of the Michigan Department of Environmental Quality with funding from the State and Tribal Wetland Development Program, Region V of the U.S. Environmental Protection Agency, Great Lakes Wetland Research Consortium of the Great Lakes Commission with funding from the Great Lakes National Program Office, and the U.S. Environmental Protection Agency.

Table 3.1

Species of anurans found in southern Michigan and included in this study. All species except *B. fowleri* are distributed throughout the study area. Species ranges were determined from Harding (1997) and Conant and Collins (1998).

Species	**Distribution**
Rana sylvatica	Statewide
Pseudacris triseriata	Statewide
Pseudacris crucifer	Statewide
Rana pipiens	Statewide
Rana palustris	Statewide
Bufo fowleri	Southern and Western Lower Michigan
Bufo americanus	Statewide
Hyla versocolor	Statewide
Hyla chrysoscelis	Statewide
Acris crepitans blanchardi	Southern Lower Michigan
Rana clamitans	Statewide
Rana catesbeiana	Statewide

Table 3.2

Summary of land cover and road variables at both spatial scales in southern Michigan. All land cover types represented the total area (m^2) within each buffer; roads represented the total length of roads within each buffer. Values are means from all study sites (N=1055), their associated standard errors, and the proportion of the total buffer area comprised by each land cover type.

Variable	**100 m**			**1000 m**		
	Mean	**SE**	**Prop.**	**Mean**	**SE**	**Prop.**
Roads (m)	211.42	2.19		7689.12	157.58	
Urban (m^2)	4941.55	119.96	0.157	279134.94	9447.15	0.089
Agriculture (m^2)	6448.53	254.63	0.205	1010738.78	23003.6	0.322
Open Land (m^2)	3607.66	107.13	0.115	345940.05	5713.59	0.110
Forest (m^2)	7608.18	215.59	0.242	826547.71	14206.76	0.263
Water (m^2)	469.63	63.15	0.015	88833.27	5529.91	0.028
Forested Wetlands (m^2)	2749.66	114.24	0.088	216686.72	5657.77	0.069
Nonfor. Wetlands (m^2)	5423.66	168.86	0.173	357936.29	7333.39	0.114

Table 3.3

Principal components retained from PCA of variables at 100 m scale. The first four principal components explained a total of 85.12% of the variation in the dataset at that spatial scale.

	PC 1	PC 2	PC 3	PC 4
Eigenvalue	6.310	3.971	2.380	1.419
Prop. Total Variance	0.3814	0.2400	0.1439	0.0858
Eigenvectors of Original Variables				
Roads	-0.00006	0.00194	0.00594	-0.00001
Urban	-0.05374	0.01013	0.02366	0.12487
Agriculture	-0.56738	0.61456	0.50623	0.14574
Open Land	-0.00562	-0.39858	0.56344	0.24481
Forest	0.10894	-0.46158	0.53646	-0.05227
Water	0.07234	-0.05914	-0.20277	0.88056
Forested Wetlands	0.60096	0.33863	0.26543	-0.20611
Nonforested Wetlands	0.54488	0.36348	0.16220	0.28747

Table 3.4

Principal components retained from PCA of landscape variables at 1000 m scale. The first two principal components explained a total of 93.66% of the variation in the dataset at that spatial scale

	PC 1	PC 2
Eigenvalue	5.772	2.314
Prop. Total Variance	0.6686	0.2680
Eigenvectors of Original Variables		
Roads	0.03153	-0.06492
Urban	0.03622	-0.08214
Agriculture	-0.21743	0.96620
Open Land	0.01687	-0.04394
Forest	0.02376	-0.04946
Water	0.97305	0.22029
Forested Wetlands	0.03361	0.03266
Nonforested Wetlands	0.04014	0.03890

Table 3.5

Significant (p<0.05) landscape factors affecting occurrence of individual anuran species at 100 m scale determined using logistic regression.

Species	**Landscape Variables**	**Regression Coefficient**	**Chi-square**	**P-Value**
Rana sylvatica	Urban	-0.255	7.532	0.006
	Agriculture	0.229	12.377	<0.001
	Nonforested wetlands	0.163	4.719	0.030
Pseudacris triseriata	Urban	0.323	4.315	0.038
	Agriculture	0.320	13.418	<0.001
	Water	-0.289	21.693	<0.001
	Forested wetlands	1.477	15.479	<0.001
	Nonforested wetlands	0.622	12.330	<0.001
Pseudacris crucifer	Urban	-2.686	13.828	<0.001
	Agriculture	-1.152	6.096	0.014
	Forest	-0.290	4.055	0.044
	Water	-0.221	4.477	0.034
	Forested wetlands	-2.079	9.765	0.002
Rana pipiens	Roads	-1.835	6.464	0.011
	Urban	-0.185	6.192	0.013
	Agriculture	0.140	15.168	<0.001
	Water	-1.878	3.962	0.047
	Forested wetlands	-1.766	9.142	0.003
	Nonforested wetlands	0.138	6.025	0.014
Rana palustris	Water	-4.549	4.726	0.030
Bufo fowleri	Urban	-0.739	6.739	0.009
	Agriculture	-0.227	5.220	0.022
	Nonforested wetlands	-0.977	5.611	0.018
Bufo americanus	Open land	-0.397	7.007	0.008
	Forested wetlands	-0.724	17.244	<0.001
	Nonforested wetlands	-0.170	6.318	0.012
Hyla versicolor/chrysoscelis	Agriculture	0.181	8.714	0.003
Acris creptians blanchardi	Agriculture	-0.691	6.574	0.010
	Water	0.204	3.895	0.048
Rana clamitans	Water	0.221	4.312	0.038
Rana catesbeiana	Urban	-0.359	4.314	0.038
	Agriculture	-0.525	8.151	0.004
	Water	0.242	18.769	<0.001
	Forested wetlands	-0.382	4.197	0.041
	Nonforested wetlands	0.135	5.346	0.021

Table 3.6

Significant ($p<0.05$) principal components affecting occurrence of individual anuran species at 100 m scale determined using logistic regression.

Species	**Principal Components**	**Regression Coefficient**	**Chi-square**	**P-Value**
Rana sylvatica	4	-0.236	13.791	<0.001
Pseudacris triseriata	2 4	-0.212 -0.328	8.233 20.765	0.004 <0.001
Rana pipiens	2	-0.126	6.574	0.010
Rana palustris	2	-0.218	5.117	0.024
Bufo americanus	1	-0.122	4.888	0.027
Hyla versicolor/ chrysoscelis	2	-0.415	10.610	0.001
Acris creptians blanchardi	4	0.633	11.793	<0.001
Rana clamitans	1	0.250	14.264	<0.001
Rana catesbeiana	1	0.211	18.528	<0.001

Table 3.7

Significant (p<0.05) landscape factors affecting occurrence of individual anuran species at 1000 m scale determined using logistic regression.

Species	**Landscape Variables**	**Regression Coefficient**	**Chi-square**	**P-Value**
Rana sylvatica	Urban	-1.625	15.088	<0.001
	Open land	4.580	10.831	0.001
	Forest	-3.813	8.206	0.004
	Forested wetlands	0.694	7.018	0.008
Pseudacris triseriata	Roads	-16..067	8.726	0.003
	Open land	1.604	9.064	0.003
	Forest	-1.044	5.309	0.021
	Nonforested wetlands	-14.958	9.108	0.003
Pseudacris crucifer	Urban	-19.788	16.152	<0.001
	Forest	2.800	15.417	<0.001
	Forested wetlands	-38.444	17.123	<0.001
	Nonforested wetlands	-13.546	7.874	0.005
Rana pipiens	Urban	-1.268	9.965	0.002
	Open land	1.246	8.460	0.004
	Forest	-1.377	14.302	<0.001
	Water	0.100	9.269	0.002
Bufo fowleri	Forest	-21.535	4.169	0.041
	Forested wetlands	-7.299	7.000	0.008
	Nonforested wetlands	-9.845	8.712	0.003
Bufo americanus	Urban	-20.889	14.354	<0.001
	Open land	1.282	7.200	0.007
	Forest	-20.075	16.568	<0.001
	Nonforested wetlands	-0.979	5.879	0.015
Hyla versicolor/chrysoscelis	Roads	-28.035	5.652	0.017
	Urban	-51.202	12.831	<0.001
	Open land	28.002	7.891	0.005
Acris creptians blanchardi	Urban	-38.221	5.747	0.017
	Water	-4.842	4.473	0.034
	Forested wetlands	-32.944	4.648	0.031
	Nonforested wetlands	-7.140	11.630	0.001
Rana clamitans	Water	-0.969	4.703	0.030
Rana catesbeiana	Urban	16.744	8.708	0.003
	Agriculture	3.883	7.965	0.005
	Open land	14.977	7.481	0.006
	Forest	10.227	9.783	0.002
	Water	1.911	4.497	0.034
	Forested wetlands	7.760	5.605	0.018

Table 3.8

Significant ($p<0.05$) principal components affecting occurrence of individual anuran species at 1000 m scale determined using logistic regression.

Species	**Principal Components**	**Regression Coefficient**	**Chi-square**	**P-Value**
Rana sylvatica	1	-0.096	5.204	0.023
	2	0.175	13.465	<0.001
Pseudacris triseriata	1	-0.103	4.128	0.042
Rana pipiens	1	-0.132	10.055	0.002
Bufo fowleri	2	0.313	4.169	0.041
Bufo americanus	1	0.099	4.153	0.042
Hyla versicolor/chrysoscelis	1	-0.254	13.631	<0.001

Table 3.9

Results of multiple regression analyses of landscape variables on anuran abundance and species richness at 100 m scale. N=1055 for all species except *B. fowleri* (N=651).

Abundance and Richness Variables	**Landscape Variables**	**Regression Coefficient**	**R^2**	**P-value**
Rana sylvatica	Urban	-0.204	0.045	<0.001
	Agriculture	0.058		0.003
	Water	-0.082		0.010
Pseudacris triseriata	Agriculture	0.044	0.034	0.015
	Water	-0.130		<0.001
Rana pipiens	Urban	-0.104	0.037	<0.001
	Agriculture	0.032		0.008
	Forest	-0.039		0.041
	Nonforested Wetlands	0.058		0.002
Bufo fowleri	Agriculture	-0.018	0.018	0.011
Bufo americanus	Water	0.088	0.016	0.002
Hyla versicolor /chrysoscelis	Roads	-0.482	0.039	0.011
	Urban	-0.092		0.008
	Agriculture	0.072		<0.001
	Water	-0.053		0.041
Rana clamitans	Urban	-0.091	0.045	0.003
	Forest	-0.054		0.016
	Water	0.070		0.002
	Nonforested Wetlands	0.053		0.018
Rana catesbeiana	Water	0.125	0.062	<0.001
	Nonforested Wetlands	0.039		0.039
Species Richness	Agriculture	0.104	0.035	<0.001
	Open Land	0.087		0.039
	Forest	-0.081		0.050
	Nonforested Wetlands	0.094		0.023

Table 3.10

Results of multiple regression analyses of Principal Components on anuran abundance and species richness at 100 m scale. N=1055 for all species except *B. fowleri* (N=651).

Abundance and Richness Variables	**Principal Components**	**Regression Coefficient**	**R-squared**	**P-value**
Rana sylvatica	4	-0.206	0.034	<0.001
Pseudacris triseriata	1	-0.048	0.026	0.048
	3	0.085		0.008
	4	-0.133		<0.001
Pseudacris crucifer	1	0.038	0.008	0.028
Rana pipiens	2	-0.052	0.016	0.003
	3	-0.048		0.027
Rana palustris	2	-0.014	0.005	0.038
Bufo fowleri	2	0.022	0.009	0.025
Bufo americanus	4	0.062	0.007	0.046
Hyla versicolor/chrysoscelis	4	-0.122	0.021	<0.001
Acris creptians blanchardi	4	0.024	0.006	0.036
Rana clamitans	1	0.100	0.034	<0.001
Rana catesbeiana	1	0.080	0.055	<0.001
	4	0.123		<0.001
Species Richness	2	-0.097	0.009	0.012

Table 3.11

Results of multiple regression analyses of landscape variables on anuran abundance and species richness at 1000 m scale. N=1055 for all species except *B. fowleri* (N=651).

Abundance and Richness Variables	Landscape Variables	Regression Coefficient	R^2	P-value
Rana sylvatica	Roads	0.658	0.099	0.024
	Urban	-1.153		<0.001
	Agriculture	0.063		0.017
	Forested wetlands	0.481		<0.001
Pseudacris triseriata	Roads	-1.145	0.075	<0.001
	Agriculture	0.065		0.010
	Open land	0.902		<0.001
	Forest	-0.387		0.024
	Forested wetlands	0.396		0.001
	Nonforested wetlands	-0.422		0.011
Pseudacris crucifer	Roads	-0.493	0.081	0.013
	Agriculture	0.043		0.018
	Forest	0.412		0.001
	Nonforested wetlands	0.269		0.025
Rana pipiens	Urban	-0.413	0.088	0.001
	Open land	0.308		0.022
	Forest	-0.478		<0.001
	Water	0.036		0.001
	Forested wetlands	0.161		0.034
Bufo americanus	Urban	-0.507	0.034	0.006
	Open land	0.799		<0.001
	Forest	-0.711		<0.001
	Water	0.060		<0.001
	Forested wetlands	0.283		0.011
	Nonforested wetlands	-0.602		<0.011
Hyla versicolor/chrysoscelis	Urban	-0.527	0.080	0.002
	Agriculture	0.098		<0.001
Rana clamitans	Agriculture	-0.066	0.041	0.001
	Water	0.045		<0.001
Rana catesbeiana	Agriculture	-0.044	0.046	0.011
	Water	0.044		<0.001
Species Richness	Agriculture	0.077	0.021	0.035
	Open land	0.760		0.011

Table 3.12

Results of multiple regression analyses of Principal Components on anuran abundance and species richness at 1000 m scale. N=1055 for all species except *B. fowleri* (N=651).

Abundance and Richness Variables	**Principal Components**	**Regression Coefficient**	**R-squared**	**P-value**
Rana sylvatica	1 2	-0.155 0.119	0.066	<0.001 <0.001
Pseudacris triseriata	1	-0.099	0.023	<0.001
Pseudacris crucifer	1 2	-0.046 0.100	0.040	0.001 <0.001
Rana pipiens	1 2	-0.095 0.075	0.068	<0.001 <0.001
Bufo fowleri	2	-0.023	0.012	0.014
Hyla versicolor/chrysoscelis	1	-0.131	0.052	<0.001
Rana clamitans	1 2	-0.037 0.074	0.019	0.020 <0.001
Rana catesbeiana	2	0.079	0.023	<0.001
Species Richness	2	0.098	0.009	0.004

Table 3.13

Temporal patterns in species richness at breeding sites in various landscape contexts. Trends indicate results from regression analyses 1996-2002.

Landscape Context	**N**	**Regression Coefficient**	**R-squared**	**P-value**
Urban	52	0.132	0.034	0.194
Agriculture	1604	0.009	0.014	0.674
Forest	454	-0.067	0.073	0.082
Wetlands	140	-0.027	0.013	0.654
Anthropogenic[1]	2134	0.003	0.011	0.891
Natural[2]	3621	-0.032	0.019	0.026

[1] Urban and agricultural landscape contexts combined

[2] Forest, wetlands, open land, and open water landscape contexts combined

Table 3.14

Results of regression analyses for temporal trends in site occupancy at breeding sites in anthropogenic and natural landscape contexts. N = 7 for all species (proportion of sites surveyed occupied by each species each year 1996-2002).

	Regression Coefficient		R- squared		P- value	
Species	**Anthropogenic**	**Natural**	**Anthopogenic**	**Natural**	**Anthropogenic**	**Natural**
Rana sylvatica	0.012	-0.001	0.163	0.001	0.370	0.969
Pseudacris triseriata	0.006	0.003	0.135	0.143	0.417	0.404
Pseudacris crucifer	0.000	-0.003	0.001	0.170	0.954	0.358
Rana pipiens	-0.004	-0.007	0.165	0.851	0.366	0.003
Rana palustris	-0.002	-0.001	0.206	0.358	0.307	0.156
Bufo fowleri	-0.001	-0.001	0.349	0.148	0.163	0.394
Bufo americanus	-0.006	-0.012	0.223	0.290	0.284	0.213
Hyla versicolor/ chrysoscelis	0.001	-0.006	0.005	0.118	0.885	0.451
Acris creptians blanchardi	-0.005	-0.004	0.667	0.477	0.025	0.086
Rana clamitans	0.003	0.004	0.015	0.074	0.792	0.556
Rana catesbeiana	0.003	0.003	0.175	0.099	0.351	0.491

Table 3.15

Results of regression analyses for temporal trends in annual call index values at breeding sites in anthropogenic (abbreviated anthro. in column headings) and natural landscape contexts.

	N		Regression Coefficient		R- squared		P- value	
Species	**Anthro.**	**Natural**	**Anthro.**	**Natural**	**Antho.**	**Natural**	**Anthro.**	**Natural**
Rana sylvatica	616	1184	0.048	0.052	0.011	0.015	0.009	<0.001
Pseudacris triseriata	1142	1728	-0.006	-0.001	0.001	0.001	0.603	0.909
Pseudacris crucifer	1685	3083	0.033	-0.001	0.070	0.001	<0.001	0.983
Rana pipiens	270	519	0.002	-0.001	0.001	0.001	0.861	0.928
Rana palustris	35	32	0.134	-0.032	0.310	0.011	0.001	0.570
Bufo fowleri	15	41	-0.005	-0.048	0.01	0.028	0.921	0.292
Bufo americanus	778	1323	-0.007	-0.032	0.001	0.071	0.607	0.002
Hyla versicolor/ chrysoscelis	1651	2588	-0.017	0.021	0.020	0.032	0.095	0.010
Acris creptians blanchardi	36	60	0.011	0.153	0.001	0.122	0.906	0.006
Rana clamitans	1213	2269	0.023	0.025	0.091	0.073	0.009	<0.001
Rana catesbeiana	280	668	0.018	-0.012	0.007	0.002	0.167	0.257

Figure 3.1

Locations of survey routes for the Michigan Frog and Toad Survey throughout Michigan.Only routes in the outlined portion of the southern lower peninsula were used in this study.

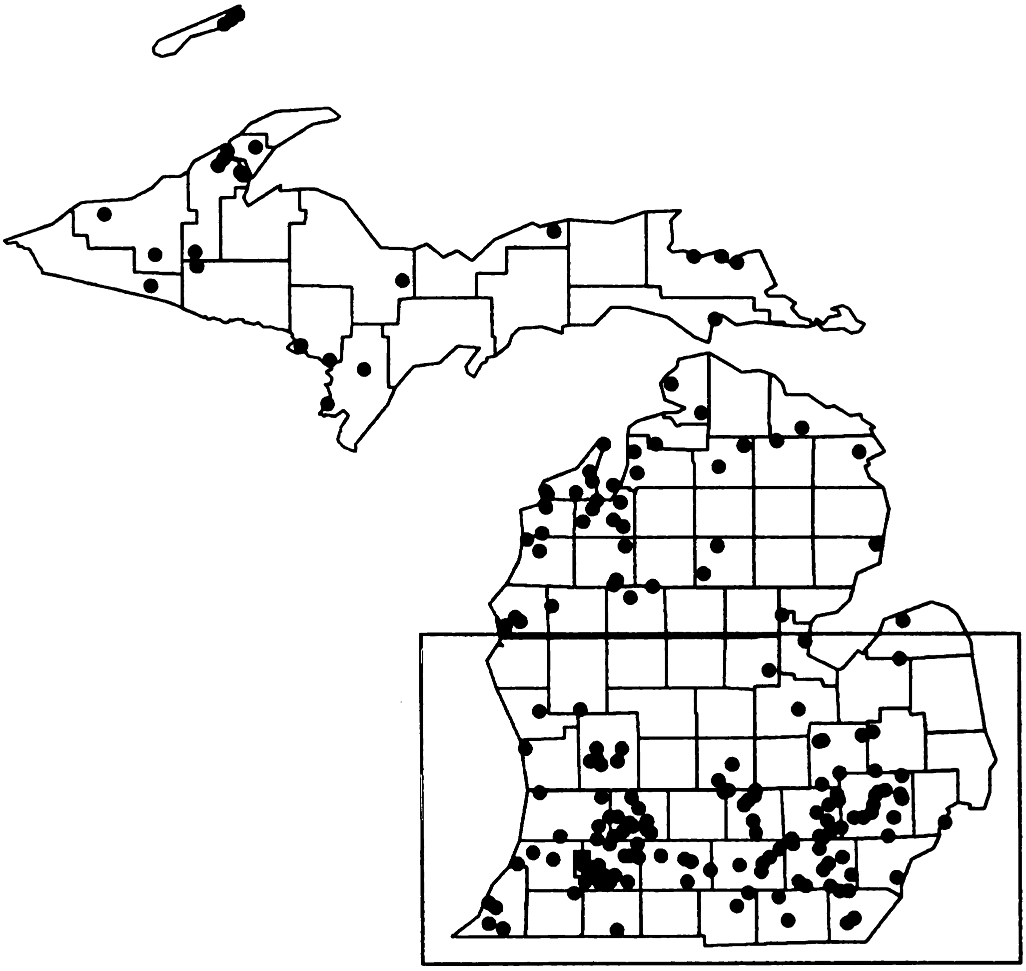


Figure 3.2

Eigenvalue plots from Principal Components Analysis at 100 m spatial scale. All three panels share the indentical X-axis. Landscape variables plotted are those described in Table 3.2. Abbreviations are as follows: ag=agriculture, open=open land, forwet=forested wetlands, nforwet=nonforested wetlands. Other variables not abbreviated.

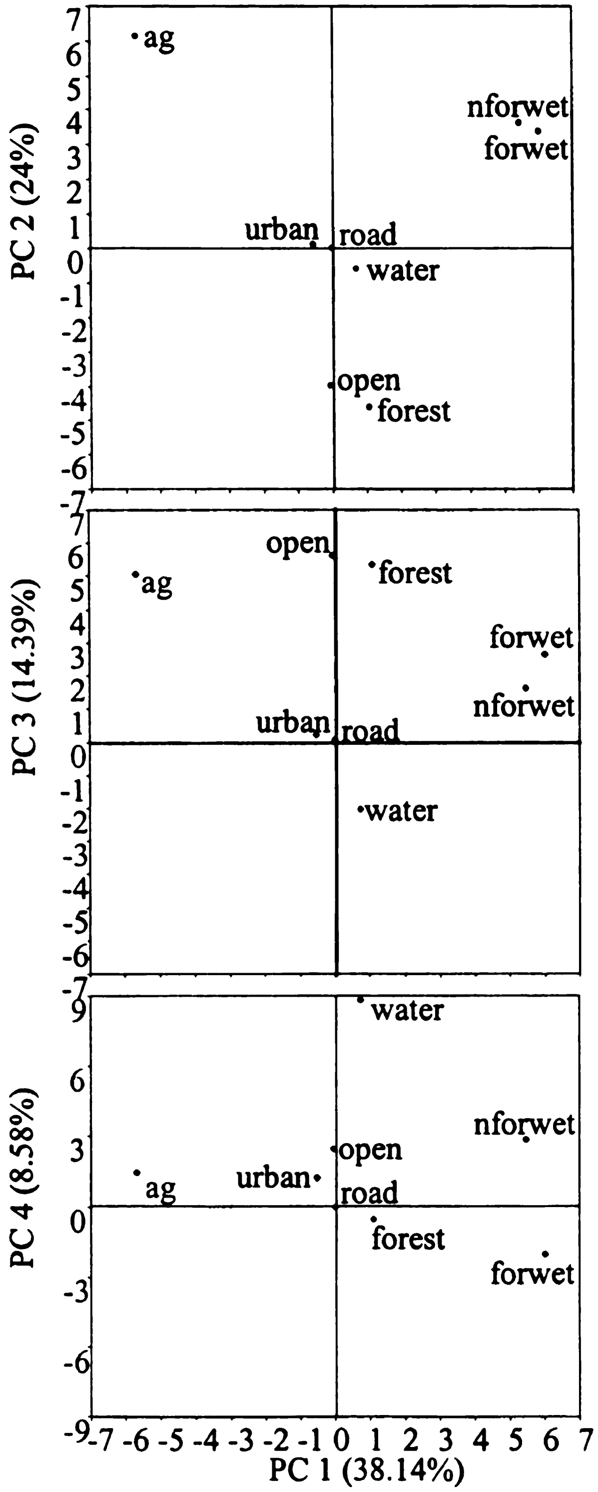


Figure 3.3

Eigenvalue plots from Principal Components Analysis at 1000 m spatial scale. Landscape variables plotted are those described in Table 3.2. Abbreviations are as follows: ag=agriculture, open=open land, forwet=forested wetlands, nforwet=nonforested wetlands. Other variables not abbreviated.

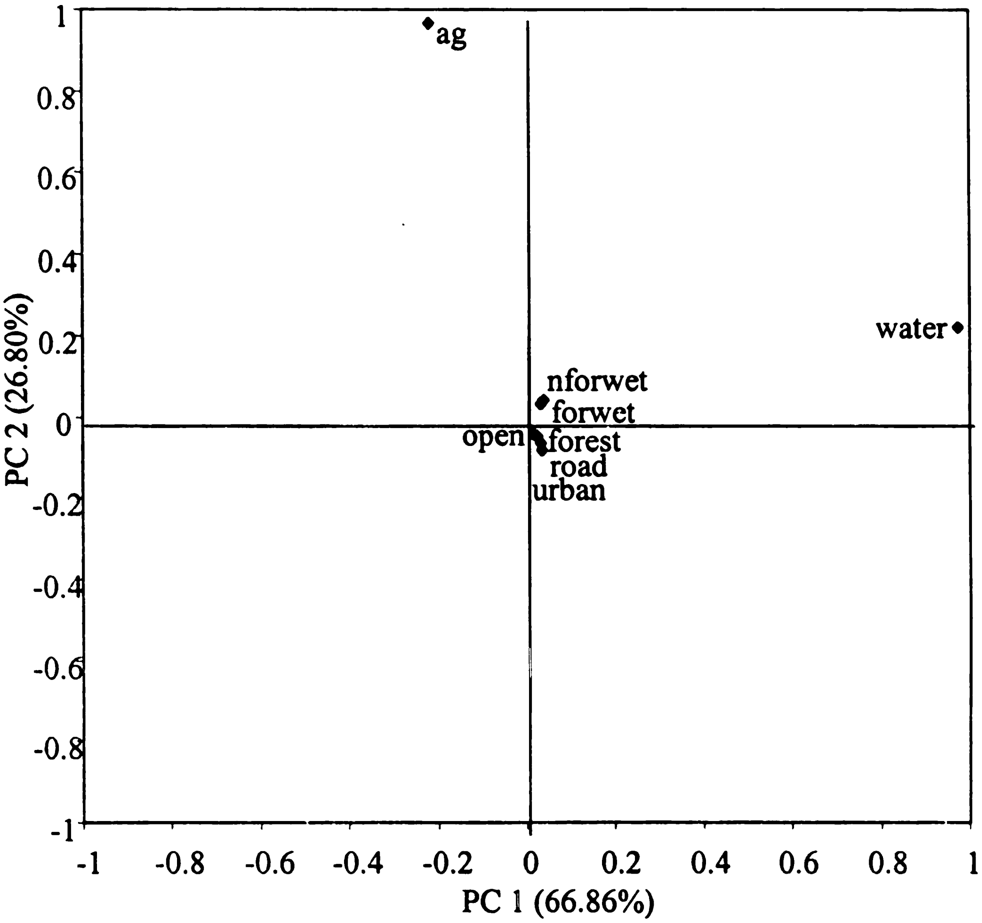


Figure 3.4

Temporal trend (1996-2002) in site occupancy for *Acris crepitans blanchardi*. Open circles indicate proportion of survey sites occupied in natural landscape contexts, and darkened circles indicate proportion of survey sites occupied in anthropogenic landscape contexts. Solid line represents significant linear trend in site occupancy in anthropogenic landscape context.

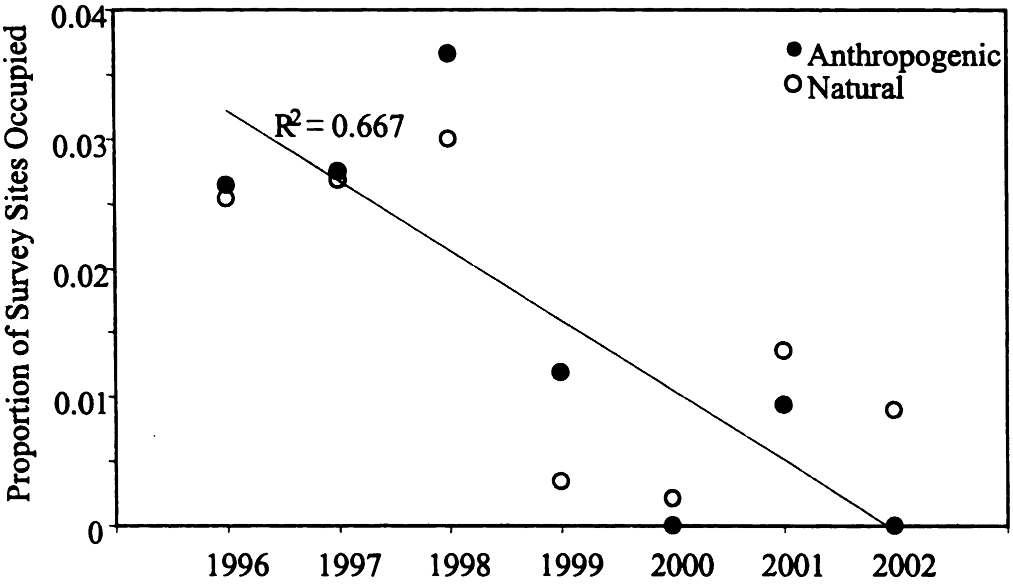
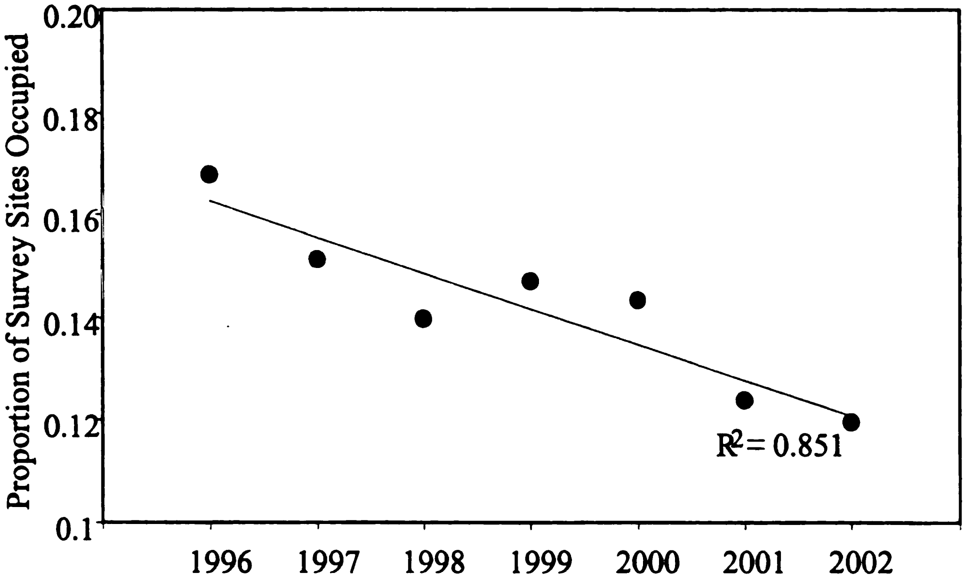


Figure 3.5

Temporal trend (1996-2002) in site occupancy for *Rana pipiens* in survey sites in a natural landscape context. Solid line represents significant linear trend in site occupancy.



Chapter Four

The Influence of Local Habitat Characteristics on the Growth, Development, and Survival of Spring Peeper (Pseudacris crucifer) Tadpoles in Southwestern Michigan

Abstract

Tadpoles are influenced by a wide variety of physical, chemical, and biological factors specific to breeding ponds during their larval periods. These factors exert profound influences over growth, development, and survival to metamorphosis, which subsequently influence adult fitness traits. The growth and development of spring peeper (*Pseudacris crucifer*) tadpoles relative to hydrology, water chemistry, and biotic interactions were monitored in a field study in ten natural wetlands in southwestern Michigan. Tadpoles in predator-free enclosures were monitored throughout their larval period for (1) growth and development rates, (2) survival, (3) length of larval period, and (4) size at metamorphosis. Growth, development, and survival were highest at sites with intermediate hydroperiods, partial canopy cover, and few fish predators. Few site-specific water chemistry variables correlated significantly with tadpole response variables, but chlorophyll *a* was significantly related to growth and size at metamorphosis. Tadpole development and metamorphosis are complex processes influenced to varying degrees by a wide variety of physical, chemical, and biological factors specific to breeding sites. Growth, development, and survival of Spring peepers varied depending upon habitat factors at each of the study sites in southwestern Michigan.

Introduction

Anuran amphibians have been widely regarded as model systems both for the experimental study of small-scale ecological processes structuring larval communities (e.g., Morin 1983, Wilbur 1987) as well as large-scale ecological patterns of metapopulation dynamics and amphibian declines (e.g., Blaustein et al. 1994a, Sjögren-Gulve 1994, Hecnar and M'Closkey 1996). Since the early 1990s, there has been increased interest, debate, and research concerning the apparent declines of amphibian populations on a global scale, although the causes have yet to be unambiguously determined (Sarkar 1996, Green 1997b, Alford and Richards 1999, Houlahan et al. 2000). Amphibians are generally considered to be sensitive indicators of environmental conditions as a result of characteristics such as complex biphasic life cycles, cutaneous respiratory surfaces, food habits, susceptibility to cold and drought, fragmented local population distributions, and vulnerability to environmental contaminants and ultraviolet radiation in both aquatic and terrestrial habitats (Stebbins and Cohen 1995).

Amphibians have complex life cycles; they are dependent on both aquatic and terrestrial habitats during distinct life history stages (Wilbur 1980). In the larval stages anurans have obligate aquatic habitat requirements. As a result, chemical and physical characteristics of the environment have the potential to exert profound effects on tadpole characteristics such as growth, development, survival, length of larval period, and metamorphic size (Alford 1999). Furthermore, the aquatic embryonic and larval stages may be the most vulnerable to mortality as both biotic and abiotic factors can act and interact to influence growth and survival of these organisms (Dunson and Travis 1991). Rates of growth, development, survival, and length of larval period also have subsequent effects on life history traits such as timing of and size at metamorphosis and juvenile recruitment, which are ultimately related to adult traits directly correlated with fitness (Wilbur and Collins 1973, Collins 1979, Werner 1986, Patterson and McLachlan 1989, Harris 1999).

Larval amphibians represent an excellent system for investigating the influence of multiple abiotic and biotic factors on life history traits, and many aspects of tadpole ecology have been studied extensively. Abiotic factors that affect tadpoles include characteristics of the local aquatic environment such as hydrology, water chemistry, and canopy cover. Hydroperiod (the amount and duration of water in a breeding pool) is one of the most important considerations for tadpoles, and they can initiate rapid development in drying ephemeral habitats (e.g., Smith-Gill and Berven 1979, Pandian and Marian 1985, Crump 1989, Patterson and McLachlan 1989, Tejedo and Reques 1994). Survival, growth rate, length of larval period, and mass at metamorphosis are all affected by the amount of water in a pond and seasonal pond persistence (e.g., Wilbur 1987, Rowe and Dunson 1995). Pond persistence exerts strong influence on community structure in wetlands where most amphibians breed (Wellborn et al. 1996, Skelly 1997). Perturbations of water chemistry influence tadpole dynamics. Increased acidity reduces survival and retards growth (e.g., Saber and Dunson 1978, Dunson and Connell 1982, Rosenberg and Pierce 1995). Nutrients and dissolved ions can affect tadpoles directly via osmoregulatory and physiological mechanisms (e.g., Ultsch et al. 1999) or indirectly by influencing the algal community upon which they graze (e.g., Kiffney and Richardson 2001). Water temperature and dissolved oxygen content also influence growth, development, and survival throughout larval development (e.g., Lucas and Reynolds

1967, Wassersug and Seibert 1975, Harkey and Semlitsch 1988). Canopy cover over breeding ponds influences the distribution of amphibian larvae, and can reduce growth rates in ponds underneath closed canopy forests (Skelly et al. 1999, Werner and Glennemeier 1999, Skelly et al. 2002).

Anurans typically breed at wetland sites with conditions appropriate for larval development. Which breeding sites are suitable differs among species and generally represent trade-offs between competition, predation, and pond permanence among different habitat types (Duellman and Trueb 1986, Skelly 1995a, 1995b, 1997, Harding 1997). Some species (e.g., *Pseudacris triseriata*) prefer ephemeral wetlands that fill with meltwater early in the spring and completely dry by the end of the summer because of the rapid nutrient flush in the spring and absence of large predators (e.g., fish) (Smith 1983, Harding 1997). Other species (e.g., *Rana catesbeiana, R. clamitans*) have physiological or behavioral defense mechanisms that allow them to exploit permanent ponds with fish predators (Harding 1997, Alford 1999).

Spring peepers (*Pseudacris crucifer*) are able to utilize a variety of temporary and semi-permanent wetlands for breeding (Skelly 1995, Harding 1997). This species is common, widespread, and stable throughout Michigan (Harding 1997, see also Chapter One). Spring Peepers are one of the earliest breeding amphibians in Michigan, and typically begin calling in March (Harding 1997). Following the breeding season, metamorphs typically begin to emerge beginning in June, but development and metamorphosis can take up to 90 days at some sites (Harding 1997). Given their distribution, status, and breeding site use, Spring peepers are excellent study organisms to evaluate the influence of biotic and abiotic factors on larval biology.

Wetlands in the midwestern United States vary greatly in the physical, chemical, and biological properties that influence amphibian breeding site selection, larval performance, and ultimately recruitment of individuals into adult anuran populations. The purpose of this study was to evaluate Spring peeper growth, development, and survival in wetlands of differing abiotic (i.e., hydroperiod and water chemistry) and biotic (i.e., potential predators) conditions. Although tadpoles typically experience significant high densities and density-dependent factors such as inter- and intraspecific competition during their larval periods(e.g., Alford 1999), the objective of this study was to examine abiotic and biotic factors other than competition. Increasing the understanding of factors that influence amphibian biology at this important larval life history stage will contribute to the conservation and management of these organisms in wetlands.

Materials and Methods

Study Sites and Habitat Characteristics

Ten natural wetlands containing resident anuran populations were selected in southwestern Michigan (Figure 4.1) that represented different habitat types, hydroperiods, and predator communities (Table 4.1). Each site was surveyed approximately once per week during the breeding and larval periods of most Michigan anurans (March – August; mean number of site visits was 10). Survey methods used to determine resident anuran communities at each site included opportunistic visual encounter surveys for adults (Crump and Scott 1994), trapping of tadpoles using 2L clear plastic funnel bottle traps (Griffiths 1985, Richter 1995, Adams et al. 1997), and call surveys (Sargent 2000, Michigan Frog and Toad Survey methodology, see also Chapter

One). Anuran larvae were identified using the taxonomic keys of Watermolen and Gilbertson (1996) and Altig et al. (1998). Relative abundance of potential invertebrate and fish predators was also determined from bottle trap samples

In addition, the following habitat variables were recorded in the field using a YSI 6000 handheld multisensor: pH, dissolved oxygen concentration (DO), percent O_2 saturation, water temperature, and specific conductance. Relative changes in water level were also recorded. A water sample was collected monthly for laboratory determination of total alkalinity, sestonic (suspended) chlorophyll *a*, available nutrients (nitrate [NO_3-N], ammonium [NH_4-N], total dissolved phosphorus [TDP], soluble reactive phosphorus [SRP, PO_4-P]), cations (Ca^{2+}, Mg^{2+}, Na^+, K^+), and anions (Cl^-, SO_4^{2-}). Upon field collection, all samples were put on ice. After returning to the lab, samples were refrigerated (for determination of alkalinity and conductivity), filtered on Gelman Supor 0.47-mm membrane filters and then refrigerated (for determination of anions), or acidified with 8 N HNO_3 (cations) until analysis.

In the laboratory, conductivity was measured using an Orion model 135 conductivity meter (Analytical Technology, Inc.). Ca^{2+}, Mg^{2+}, Na^+, and K^+ were measured by flame atomic absorption spectrometry. Alkalinity, which generally represents HCO_3^- in local waters, was determined by titration with 0.3 N HCl and calculation of the Gran function (Cantrell et al. 1993). SO_4^{2-}, Cl^-, and NO_3^- were measured by membrane-suppression ion chromatography. NH_4^+ was measured colorimetrically following an adapted version of the phenylhypochlorite method (Aminot et al. 1997). Soluble reactive phosphorus (PO_4-P) and total dissolved phosphorus (TDP) were measured colorimetrically following the acid molybdate method (Wetzel and Likens

2000); the TDP colorimetric analysis was preceded by a persulfate digestion to decompose organically bound P (Valderrama 1981). Algal biomass was measured as chlorophyll-*a* fluorescence (Welshmeyer 1994) after cold extraction in 95% ethanol.

Canopy cover was recorded at each enclosure (see below) in four cardinal directions in May (Spring, beginning of leaf-out) and July (Summer, leaf-on) using a spherical densiometer (Forestry Suppliers, Inc.).

Field Study of Tadpole Growth

Two pairs of amplexed Spring peepers were collected on 5 May 2000 from a small pond in Meridian Township, Ingham County, Michigan. Frogs were brought into the laboratory until the eggs were laid and fertilized; adults were then returned to the site where they were collected. The eggs hatched after approximately one week, and hatchlings were maintained in the laboratory until they had reached approximately stage 25 (Gosner 1960). At the beginning of the field study, tadpoles from the two clutches were mixed and randomly divided into 30 groups of 10 tadpoles each. All tadpoles were measured (snout – vent body length, SVL, mm) and staged (Gosner 1960) at the beginning of the study.

Three field enclosures were placed at each of the 10 study sites. Enclosures were constructed from 19 L plastic buckets with screened sides (fiberglass insect screening) and a flotation device attached to the top. Approximately 3 cm of sediment and detritus from each study site was added to the bottom of each enclosure to provide a natural substrate and food resource for the tadpoles. Sediment and detritus were visually examined before placement in the enclosures to exclude macroinvertebrates.

On 2 June 2000, each enclosure was stocked with 10 tadpoles (0.526/L). This density was low compared to natural densities of tadpoles (Alford 1999) such that growth and development would not be influenced by density-dependent factors. In natural temporary pond environments, tadpoles may experience local densities of 25+/L (Alford 1999). Although tadpoles naturally encounter significant density-dependent factors during their larval period, the objective of this study was to evaluate growth, development, and survival relative to other environmental influences. Initial size (SVL) of tadpoles did not differ among the 10 study sites (Kruskal-Wallis ANOVA, $H = 13.133$, $p = 0.157$) and tadpoles in all enclosures were approximately stage 26 (range 24 – 31) (Gosner 1960). After fish and turtle predation eliminated all three enclosures at one site (Eagle Pond) and single enclosures at two other sites (Lawrence Lake Marsh and Jackson Hole Outflow), the tops of the enclosures were screened to exclude predators and retain froglets as they neared metamorphosis. Since all tadpoles were lost at Eagle Lake, this site was omitted from all data analyses.

Tadpoles were measured (SVL, mm) and staged in the field at approximately weekly intervals (5 – 7 days). Measurements were made in the field using a plastic petri dish marked with a 2 mm grid, which minimized handling of the tadpoles. Upon reaching metamorphosis (forelimb emergence, stage 42, Gosner 1960), tadpoles were released at each site. Tadpole response variables included (1) growth rates (mm/day; determined at weekly intervals), (2) development rates (stage/day; determined at weekly intervals), (3) total growth (mm; length at metamorphosis – length at beginning of study), (4) length of larval period (number of days from beginning of study to metamorphosis), (5) size at metamorphosis (SVL at metamorphosis), and (6) survival (proportion surviving to metamorphosis, adjusted for tadpoles lost to known sources of predation). In addition, an overall measure of the rates of growth (mm/day) and development (stage/day) was calculated as the mean increase in length (or stage) per day over the entire larval period. This study was approved for ethical appropriateness and humane handling of animals by the All University Committee on Animal Use and Care at Michigan State University (permit #77585).

Statistical Analyses

All variables were assessed for normality by evaluating goodness-of-fit tests (Kolmogorov-Smirnov procedure) and normal probability plots (Zar 1998). Variables not meeting assumptions of normality were transformed prior to statistical analyses. Most variables met assumptions without transformation, but the following variables were log (x+1) transformed: chlorophyll *a*, NH_4-N, TDP, SRP, K^+, Cl^-, and SO_4^{2-}. Proportion variables (i.e., canopy cover, tadpole survival) were arcsine transformed prior to analyses (Zar 1998). Nonparametric statistics or other methods robust to the violation of assumptions were used given the small sample size (n = 10 study sites, n = 3 enclosures per site).

Correlations between species richness and habitat variables (water chemistry, canopy cover) were evaluated using Spearman rank-correlation analyses (Zar 1998). Similarly, correlations between tadpole response variables (total growth, size at metamorphosis, length of larval period, and survival) and site-specific habitat/water chemistry variables were also evaluated using rank-correlation analyses. Tadpole growth rates and development rates were assessed relative to canopy cover, pond permanence, and presence of fish predators using Profile Analysis, a special case of multivariate analysis of variance (MANOVA) and repeated measures analysis (O'Brien and Kaiser 1985, von Ende 1993). For profile analysis of the influence of canopy cover on tadpole response variables, sites were classified as either open canopy (<25% canopy cover; Lawrence Lake March, Cobb-Pifer Marsh, Lux Arbor Pond 28), partial canopy (26-74% canopy cover; Jackson Hole Outflow, Douglas Lake Outflow, Loosestrife Pond, Duckweed Pond), or closed canopy (>75% canopy cover; Maple Pond, Wood Frog Pond). All data analyses were performed using SYSTAT (version 8.0, SPSS, Inc. 1998) and SAS (release 8.02, SAS Institute 2002).

Results

Resident Anuran Community

The species richness of resident anurans ranged from 2 – 8 among the 10 study sites (Table 4.2). Fowler's toads (*Bufo fowleri*) and Pickerel frogs (*Rana palustris*) were not detected calling or by opportunistic visual encounters during the field study at any of the sites. The two morphologically identical species of Gray treefrogs (*Hyla versicolor* and *H. chrysoscelis*) were combined into one composite treefrog species, as the calls are difficult to distinguish, and temperature can affect the pulse rate and duration of their calls, making them very difficult to identify in single species choruses (Harding 1997). Spring peepers (*P. crucifer)* were detected at 6 of the 10 study sites; they were absent from the four largest permanent ponds.

Species richness at the sites was not correlated with any of the water chemistry or hydrology variables (Spearman Rank Correlation, $p > 0.05$). Canopy cover shading each site varied from <5% - >90% (Table 4.1). Species richness was also unrelated to percent canopy cover ($r_s = -0.056$; $p > 0.5$).

Habitat and Water Chemistry Characteristics of Sites

The study sites differed significantly with respect to water chemistry and hydrology (Table 4.3, Appendix 4.1). The study sites could be arranged along a continuum representing wetlands that were primarily precipitation-fed to those that were predominantly groundwater-fed using Mg^{2+} and specific conductance as indicators of water sources (Figure 4.2). In this area, Mg^{2+} and specific conductance strongly covary because of the influence of dolomite weathering on major ion composition, but Mg^{2+} is a better indicator of groundwater (S.K Hamilton, pers. comm.). Sites also varied with respect to water level fluctuations, although Maple Pond was the only site that dried completely during this study (Appendix 4.1). Bottle trap samples detected the presence of predatory fish in six of the ten study sites, but only Eagle Pond had predatory fish comprising >5% of the total community (Figure 4.3). Predatory fish species included Bluegill (*Lepomis macrochirus*), Green sunfish (*Lepomis cyanellus*), Pumpkinseed (*Lepomis gibbosus*), and Largemouth bass (*Micropterus salmoides*). Invertebrate predators were the dominant predation threat for tadpoles at most sites. Water chemistry variables differed significantly among sites (Table 4.3). Nitrate (NO_3-N) was below detection limits of ca. 0.01 mg/L in most samples, and was therefore omitted from further analyses. Many variables also differed significantly among months during the sampling period (Water Temp., NH_4-N, TDP, and SO_4^{2-}; Kruskal-Wallis ANOVA, $p<0.05$) (Table 4.3). Three of those variables had significant linear trends over time. Water temperature and ammonium (NH_4-N) increased during the sampling period (water temperature: $r^2=0.441$, $p<0.001$; NH_4-N: $r^2=0.597$, $p<0.001$) and SO_4^{2-} decreased ($r^2=0.288$, $p=0.004$).

Tadpole Response Variables

The total length of larval period was marginally different among sites (Kruskal-Wallis ANOVA, H=15.129, p=0.057). Tadpoles at Jackson Hole Outflow reached metamorphosis in the shortest amount of time (Table 4.4). At Maple and Wood Frog Ponds, some tadpoles had not reached metamorphosis before the ponds completely dried, and tadpoles at Lux Arbor Pond 28 had the longest larval period (Table 4.4). At metamorphosis (stage 42, forelimb emergence, Gosner 1960), size (SVL) did not differ significantly among sites (Kruskal-Wallis ANOVA, H=9.625, p=0.292). When tadpole predation from known sources (i.e., fish and turtles getting into enclosures) was considered and survival was adjusted for the remaining tadpoles at all study sites, survivorship did not differ significantly among study sites (Kruskal-Wallis ANOVA, H=12.212, p=0.142). All enclosures were eliminated from Eagle Pond, and that site was omitted from further analyses of tadpole response variables. Survivorship was highest in Cobb-Pifer Marsh, and lowest in the two lake outflow sites, Jackson Hole Outflow and Douglas Lake Outflow (Table 4.5). Both growth and development rates averaged over the course of the study differed significantly among study sites (Kruskal-Wallis ANOVA; growth rate: H=16.640, p=0.034; development rate: H=15.682, p=0.047). Tadpoles grew and developed most rapidly at Jackson Hole Outflow, and slowest at Maple and Wood Frog Ponds, respectively (Table 4.6). Generally, growth rates (divided into roughly weekly intervals) were highest at sites with warmer water temperatures, particularly in early stages of the larval period (Figure 4.4).

There were very few significant correlations between habitat and water chemistry variables during the months of the field study and tadpole response variables (Table 4.7 – 4.8). Chlorophyll *a* concentration in July was positively correlated with total growth (r_s=0.967, p<0.001, Table 4.7), size at metamorphosis (r_s=0.833, p= 0.010, Table 4.7), and overall growth rate (r_s=0.783, p<0.05, Table 4.8). Canopy cover was negatively correlated with overall growth rate (r_s= - 0.700, p<0.05).

Tadpole Growth and Development Profile Analysis

The slopes of tadpole growth rates (mm/day) over the five-week study period did not differ significantly among pond permanence categories based on Profile Analysis (F = 1.03, p = 0.485; Figure 4.5a). Growth rates were relatively constant for the duration of the study in all pond permanence categories (F = 6.81, p = 0.074). There was a significant difference among pond types in growth rate between week 1 and week 2 (F = 7.05, p = 0.027); however, no other contrasts of growth rates between successive weeks of the study were significant. Similarly, canopy cover was not a significant influence on tadpole growth rates (Figure 4.5b). The slopes of the profiles of tadpole growth rates over time did not differ with respect to the three categories of canopy cover (F = 0.92, *p* = 0.543) and growth rates were relatively constant over time (F = 7.35, *p* = 0.067). Although growth rates did not differ over the entire duration of the experiment among canopy cover categories, there was a canopy cover effect on growth rate between the first two weeks (F = 6.67, *p* = 0.029). The presence of fish did not affect the slope of the tadpole growth rate profile over time (Figure 4.5c; F = 0.29, *p* = 0.871). However, growth rates of tadpoles did decrease over the duration of the study both in the presence and absence of fish predators (Figure 4.5c; F = 10.64, *p* = 0.021).

The slopes of the curves of development rate (stage/day) over the five-week period of the study did not differ significantly with respect to pond permanence category (Figure 4.6a; F = 3.2, p = 0.059). In all pond types, development rate was relatively constant over time (F = 2.98, p = 0.197). Although there was no significant time effect overall, when each interval between sampling periods was considered separately, development rates differed between week 1 and 2 among pond types (F = 8.78, p = 0.017). Canopy cover also had no significant influence on the slope of tadpole development rate curves over time (Figure 4.6b; F = 1.33, p = 0.349), and development rates were constant over the duration of the study (F = 3.83, p = 0.150). Development rates were slower in closed canopy sites in the interval between weeks 1 and 2 (F = 11.29, p = 0.015), but no other time intervals showed significant differences among canopy cover classes. The presence of fish did not affect the slopes of the development rate curves over time (Figure 4.6c; F = 4.43, p = 0.089). However, development rates differed significantly over the duration of the study both in the presence and absence of potential fish predators (F = 8.12, p = 0.033). There was a significant difference in development rates between weeks 1 and 2 with respect to the presence of fish predators (F = 11.66, p = 0.011).

Discussion

Spring peepers utilize a wide variety of wetland types for successful breeding, including both ephemeral and permanent ponds. However, this species is typically less abundant in ephemeral ponds that dry each year relative to other anurans (e.g., *Pseudacris triseriata*, Western chorus frogs) and more abundant in ponds with longer hydroperiods (Skelly 1995b, 1996). In this study, Spring peeper growth and development rates were lowest and length of larval period was longest in the two ponds with the shortest hydroperiods (Wood Frog Pond and Maple Pond). On the other end of the hydroperiod continuum, however, tadpole response variables also did not respond favorably to conditions in the most permanent ponds, with low growth rates, long larval periods, and low survival at permanent ponds and lake outflows. Wetlands with intermediate hydroperiods appeared to represent the balance of physical, chemical, and biotic conditions that optimized Spring peeper growth, development, and successful metamorphosis.

The two temporary pond sites with the lowest growth and development rates also had closed forest canopies shading virtually the entire surface of the breeding pond. Increased canopy cover indirectly influences tadpoles by reducing other variables important for growth, development and metamorphosis (e.g., Wassersug and Seibert 1975, Harkey and Semlitsch 1988, Werner and Glennemeier 1999, Skelly et al. 2002). Shading of breeding ponds also affects tadpole performance, primarily as a function of temperature and resource differences (Werner and Glennemeier 1999). Water temperature exerts a particularly strong influence on tadpole growth and development (e.g., Lucas and Reynolds 1967, Harkey and Semlitsch 1988). Typically, Spring peepers are only found breeding in open canopy ponds (Harding 1997, Skelly et al. 2002). Indeed, canopy closure has been hypothesized as an important factor contributing to the distribution of many species of anurans in Michigan (Werner and Glennemeier 1999, Skelly et al. 2002). Many factors probably contributed to the low rates of growth and development and long larval periods at these sites. The predominant influential factor was most likely water temperature, but other factors such as canopy cover, relatively low oxygen availability, and sestonic chlorophyll *a* also played a role. Growth and development are both influenced by temperature, however, development rates are lower than growth rates at low temperatures, such that tadpoles could grow more with each developmental stage and ultimately metamorphose at a larger body size (Smith-Gill and Berven 1979).

Although there were very few significant correlations between habitat/water chemistry variables and tadpole response variables, sestonic chlorophyll *a* was significantly positively associated with most tadpole response variables. Chlorophyll *a* is an indication of resource availability. Spring peeper tadpoles ingest both suspended and attached algae, as well as occasionally supplementing their diets with detritus (Alford 1999). Higher resource levels in the form of more abundant (or higher quality, a variable not tested in this study) food sources leads to faster growth and development and larger metamorphs (Steinwascher and Travis 1983, Kupferberg et al. 1994, Kupferberg 1997).

Although the three factors evaluated in the profile analysis (pond permanence, canopy cover, and presence of fish predators) have been previously reported to influence tadpole performance (e.g., Kats et al. 1988, Skelly 1996, Loman 2002, Skelly et al. 2002), there were very few significant relationships between those variables and tadpole response variables in this study. These results are likely due to small sample sizes and thus reflect the lack of statistical power to empirically determine significant relationships. The small sample size and unbalanced design also precluded the calculation of interactions among these three factors. A qualitative examination of the tadpole growth and development profiles indicated that growth and development rates in the early portion of the larval period were reduced in temporary ponds with closed canopies, and development rates were higher in ponds with fish predators. These patterns, although not statistically significant, can be interpreted with respect to their biological significance.

Growth and development of Spring peepers varied depending upon habitat factors at each of the study sites in southwestern Michigan; however, a few issues need to be considered in the evaluation of these results. The results of the statistical analyses coupled with qualitative examination of patterns in the data indicate that I did not have a sample size large enough to have enough power to detect significant differences in rates of growth or development using the repeated measures techniques employed here. Maxwell and Delaney (1990) suggested that these statistical techniques are only appropriate when sample size is larger than conditions often allow in ecological systems. If α were set higher (i.e., 0.10) to compensate for low statistical power (Stevens 1992), differences in growth and development rates among sites over the course of this experiment would be significant. This indicates the need to evaluate ecological experiments thoroughly to address issues of both statistical and biological significance.

Although not quantified directly, predation appears to be a factor excluding Spring peepers from permanent ponds such as Eagle Pond and Jackson Hole Outflow. Even when predators were excluded from field enclosures, tadpoles in permanent ponds with predators suffered relatively high mortality and slow rates of growth while development proceeded relatively rapidly (e.g., Lux Arbor Pond 28, Douglas Lake Outflow). These tadpoles may be responding to chemical cues in the water from potential predators (Smith and van Buskirk 1995, van Buskirk 2000). Spring peepers in other semi-permanent or permanent bodies of water had high survival and relatively rapid rates of growth and development (Cobb-Pifer Marsh, Lawrence Lake Marsh and Jackson Hole Outflow). Other biotic interactions are also very important in understanding the larval biology of Spring peepers. This species is considered by many to be a competitively inferior species (i.e., Morin 1983, Skelly 1995a, 1995b). However, previous experimental results have been somewhat equivocal. While this study did not evaluate the effects of any predation or competition interactions, growth and development appeared to be complex processes that responded to potential biotic factors in addition to the habitat variables that were measured in this study.

In this study, growth, development and survival were optimized in semi-permanent wetlands. Complex factors (perhaps related to perceived predation threat and other interactions between biotic and abiotic factors) reduced Spring peeper growth and survival in permanent ponds, while the tadpoles were unable to complete development and metamorphose in temporary ponds before they dried. These factors (predation and pond drying) have been shown to be important in the distribution and abundance of this species (Skelly 1995a, 1996). The length of their larval period was also optimized in ponds of intermediate hydroperiods; metamorphosis occurred later in both permanent and temporary ponds.

Anuran larval dynamics and metamorphosis have been topics of intensive research for decades. While models that incorporate various factors in the larval environment have been developed to predict timing of and size at metamorphosis (i.e., Wilbur and Collins 1973, Collins 1979, Werner 1986), the results of this study and others in recent years indicate that tadpole development and metamorphosis are complex processes influenced to varying degrees by a wide variety of factors specific to breeding sites. Spring peeper tadpoles in southwestern Michigan responded to habitat characteristics, water chemistry, and biotic factors by altering their growth and development throughout their larval period. While this species can complete development and metamorphose from wetlands at both ends of the hydroperiod continuum, a wide variety of factors (such as temperature, canopy cover, resource availability, and fish vs. invertebrate predators) contributed to optimal growth and development at sites of intermediate hydroperiods, where tadpole survival to metamorphosis was the greatest.

Acknowledgements

Financial support for this project was graciously provided by the Michigan Chapter of The Nature Conservancy, and NSF Research Training Grant from Kellogg Biological Station. Funding was also provided by the U.S. National Science Foundation (DEB-9701714). J. A. Genet, K.B. Kiehl and W.R. Hilgris assisted with field data collection. M. Machavaram and S. K. Hamilton assisted with laboratory analyses of water samples. C. A. Lepczyk and W. Gordon provided valuable comments on earlier drafts. All animals were handled in accordance with the All University Committee on Animal Use and Care permit number 77585.

Table 4.1
Characteristics of the 10 study sites in southwestern Michigan

Site	Coordinates[1]	Landscape Context[2]	Pond Permanence[3]	Predator Community[4]	Canopy Cover[5]
Wood Frog Pond	42.321°N, 85.358°W	Forest	Temporary	Invertebrate	93.2 (1.1)
Maple Pond	42.319°N 85.358°W	Forest	Temporary	Invertebrate	91.1 (1.2)
Jackson Hole Outflow	42.315°N 85.255°W	Forest, Open Land[6], Lake	Permanent	Fish/Invertebrate	45.9 (23.2)
Eagle Pond	42.324°N 85.318°W	Forest	Permanent	Fish/Invertebrate	46.8 (11.6)
Duckweed Pond	42.329°N 85.344°W	Forest	Semi-permanent	Invertebrate	57.1 (5.8)
Douglas Lake Outflow	42.357°N 85.366°W	Forest, Lake	Permanent	Fish/Invertebrate	65.8 (13.0)
Lawrence Lake Marsh	42.441°N 85.356°W	Lake, Open Land[6]	Permanent	Fish/Invertebrate	23.3 (11.9)
Lux Arbor Pond 28	42.494°N 85.452°W	Lake, Forest	Permanent	Fish/Invertebrate	21.9 (7.8)
Loosestrife Pond	42.368°N 85.361°W	Open Land[6], Forest	Permanent	Invertebrate	49.3 (9.4)
Cobb-Pifer Marsh	42.499°N 85.344°W	Agriculture, Forest	Semi-permanent	Fish/Invertebrate	12.0 (2.4)

[1] Latitude and longitude coordinates estimated from USGS standard digital orthoquadrangles

[2] land cover types directly adjacent to the study site

[3] general seasonal pattern of inundation

[4] potential predators present in breeding ponds included Bluegill, Green sunfish, Pumpkinseed, and Largemouth Bass

[5] Percent canopy cover (std. error) in July (leaf-out) measured with a spherical densiometer

[6] open land (<25% tree cover) including parks, recreation areas, upland shrubs, and low-density trees

Table 4.2

Resident anuran community composition at field study sites. *Hyla versicolor* and *H. chrysoscelis* were combined and counted as a single species.

Species	Cobb-Pifer Marsh	Douglas Lake Outflow	Duckweed Pond	Eagle Pond	Jackson Hole Outflow	Lawrence Lake Marsh	Loosestrife Pond	Lux Arbor Pond 28	Maple Pond	Wood Frog Pond
Rana sylvatica	X		X				X		X	X
Pseudacris triseriata	X		X						X	X
Pseudacris crucifer	X		X		X		X		X	X
Rana pipiens	X		X		X				X	
Rana palustris										
Bufo fowleri										
Bufo americanus	X					X	X			
Hyla versicolor/ chrysoscelis	X		X							
Acris crepitans blanchardi					X					
Rana clamitans	X	X	X	X	X	X	X	X	X	X
Rana catesbeiana	X	X		X	X	X	X	X		
Species Richness	8	2	6	2	5	3	5	2	5	4

Table 4.3

Water chemistry variables at field study sites, measured monthly during anuran breeding and larval period (March – July, n = 5 samples for all variables except chl α, where n = 4). Values represent mean (std. error) for each site, and variables that differed significantly among sites are indicated by asterisks (Kruskal-Wallis ANOVA; *$p<0.05$, **$p<0.01$, ***$p<0.005$, ****$p<0.001$).

	Cobb-Pifer Marsh	**Douglas Lake Outflow**	**Duckweed Pond**	**Eagle Pond**	**Jackson Hole Outflow**	**Lawrence Lake Marsh**	**Loosestrife Pond**	**Lux Arbor Pond 28**	**Maple Pond**	**Wood Frog Pond**
Water Temp (°C)	16.00 (2.20)	16.76 (2.27)	14.11 (1.66)	18.96 (1.48)	19.15 (0.94)	20.81 (3.41)	15.17 (2.45)	18.76 (3.90)	14.13 (1.26)	12.73 (1.92)
****DO (mg/L)	9.18 (1.06)	10.03 (0.53)	3.33 (1.54)	10.35 (0.74)	9.98 (1.21)	13.02 (0.82)	10.85 (2.63)	11.63 (0.85)	4.37 (1.19)	1.82 (0.48)
****O_2 Sat. (%)	91.72 (7.92)	103.06 (6.24)	31.46 (1.54)	110.80 (5.68)	107.90 (13.20)	146.48 (15.76)	110.32 (31.51)	124.54 (12.02)	42.58 (11.75)	16.78 (4.10)
Chl *a* (ug/L)	13.63 (3.79)	8.19 (3.76)	13.13 (8.72)	7.12 (1.61)	11.39 (2.76)	6.42 (1.16)	5.27 (1.82)	4.83 (0.84)	2.71 (1.02)	12.03 (6.33)
****pH	7.09 (0.03)	8.00 (0.07)	7.32 (0.09)	8.12 (0.12)	7.88 (0.18)	8.9 (0.41)	8.77 (0.42)	8.31 (0.09)	7.41 (0.05)	7.01 (0.04)
****Alkalinity (ueq/L)	590.70 (59.16)	3613.92 (112.71)	2577.79 (47.29)	2865.2 (107.95)	3491.22 (213.73)	2865.71 (189.84)	2740.59 (181.9)	1985.26 (188.16)	2938.23 (197.52)	1075.92 (176.72)
****Specific Conductance (uS/cm)	91.8 (5.3)	378.8 (9.0)	276.6 (6.6)	284.8 (7.3)	368 (18.1)	271.8 (19.5)	311.6 (23.3)	210.2 (17.2)	338 (36.5)	114.6 (21.2)

NH_4-N (ug N/L)	7.41 (0.65)	5.30 (1.44)	8.10 (4.04)	6.68 (0.64)	76.72 (66.66)	45.34 (31.14)	8.97 (2.21)	66.34 (32.09)	8.52 (1.76)	97.81 (60.89)
**SRP (ug/L)	10.08 (1.15)	6.41 (1.04)	29.48 (5.44)	5.13 (0.50)	48.21 (40.6)	7.73 (0.95)	6.27 (0.83)	5.8 (0.81)	10.26 (1.82)	327.03 (52.74)
***TDP (ug/L)	39.55 (8.06)	15.04 (5.53)	38.96 (2.88)	21.26 (6.22)	21.02 (3.06	24.14 (3.34)	15.22 (2.25)	46.62 (26.8)	67.81 (39.26)	374.93 (53.87)
*Ca^{2+} (mg/L)	12.41 (1.04)	48.47 (2.14)	42.66 (0.84)	43.93 (0.69)	48.2 (2.6)	30.46 (2.83)	37.69 (2.67)	29.66 (3.45)	62.17 (6.49)	18.28 (1.44)
****Mg^{2+} (mg/L)	4.13 (0.33)	20.34 (0.37)	11.92 (0.5)	13.11 (0.53)	20.09 (0.98)	19.92 (1.41)	18.09 (1.39)	9.24 (0.68)	7.32 (0.51)	5.68 (0.57)
****Na^+ (mg/L)	3.79 (0.13)	6.52 (0.29)	2.38 (0.28)	1.54 (0.09)	4.27 (0.34)	2.06 (0.29)	5.62 (0.5)	2.79 (0.4)	1.89 (0.15)	1.22 (0.08)
****K^+ (mg/L)	0.99 (0.08)	0.85 (0.23)	0.76 (0.15)	0.15 (0.05)	0.93 (0.12)	0.59 (0.25)	0.54 (0.24)	0.67 (0.22)	2.99 (0.39)	2.97 (0.26)
****Cl^- (mg/L)	4.87 (0.67)	10.76 (0.48)	5.24 (0.57)	1.83 (0.11)	7.09 (0.57)	3.13 (0.56)	11.04 (1.66)	4.74 (0.54)	2.55 (0.43)	1.20 (0.08)
*SO_4^- (mg/L)	4.20 (2.03)	10.88 (0.78)	10.38 (3.43)	8.31 (0.37)	16.04 (5.19)	5.41 (1.06)	17.23 (2.11)	3.98 (1.05)	34.27 (20.48)	10.41 (4.2)

Table 4.4

Mean length of larval period (days) for Spring peeper tadpoles at field study sites. Length of larval period was defined as the number of days between the beginning of the experiment (2 June 2000, day 0) and the day the tadpoles metamorphosed (stage 42, forelimb emergence).

Site	**Days** Mean (std. error)
Cobb-Pifer Marsh	36.7 (1.5)
Duckweed Pond	38.8 (3.1)
Lawrence Lake Marsh	30.5 (1.2)
Loosestrife Pond	33.6 (0.6)
Lux Arbor Pond 28	48.1 (3.1)
Wood Frog Pond	46.3 (2.2)
Jackson Hole Outflow	26.7
Douglas Lake Outflow	41.4 (5.9)
Maple Pond	46.0 (1.5)

Table 4.5

Mean survivorship of Spring peeper tadpoles at study sites during field study. Survival represents the mean survival of all enclosures at a site (n=3 for all sites except Lawrence Lake Marsh and Jackson Hole Outflow, where n=2). Enclosures where fish or turtles completely depredated tadpoles were eliminated from further analyses (all enclosures were eliminated from Eagle Pond).

Site	**Survival** Mean (std. error)
Cobb-Pifer Marsh	0.726 (0.175)
Duckweed Pond	0.293 (0.136)
Lawrence Lake Marsh	0.639 (0.139)
Loosestrife Pond	0.300 (0.200)
Lux Arbor Pond 28	0.178 (0.097)
Wood Frog Pond	0.500 (0.058)
Jackson Hole Outflow	0.150 (0.150)
Douglas Lake Outflow	0.161 (0.061)
Maple Pond	0.463 (0.067)

Table 4.6

Overall rates of growth (mm/day) and development (stage/day) for larval Spring peepers at field study sites in southwestern Michigan averaged over entire larval period (enclosure stocking to metamorphosis). Both growth and development rates differed significantly among sites (Kruskal-Wallis ANOVA, $p < 0.05$).

Site	**Growth Rate mm/day (SE)**	**Development Rate stage/day (SE)**
Cobb-Pifer Marsh	0.228 (0.009)	0.479 (0.015)
Duckweed Pond	0.213 (0.014)	0.446 (0.030)
Lawrence Lake Marsh	0.225 (0.030)	0.561 (0.019)
Loosestrife Pond	0.204 (0.008)	0.457 (0.039)
Lux Arbor Pond 28	0.171 (0.021)	0.415 (0.012)
Wood Frog Pond	0.169 (0.007)	0.352 (0.008)
Jackson Hole Outflow	0.302 (0)	0.710 (0)
Douglas Lake Outflow	0.163 (0.008)	0.421 (0.077)
Maple Pond	0.151 (0.002)	0.355 (0.005)

Table 4.7

Correlations between habitat and water chemistry parameters and tadpole response variables. Values are Spearman Rank Correlation coefficients (r_s). Significance in indicated by asterisks ($^*p<0.05$ $^\dagger p<0.10$).

	Total Growth (mm)[1]		Length of Larval Period (Days)[2]		Survival (Prop.)[3]		Size at Metamorphosis (mm)[4]	
	June	July	June	July	June	July	June	July
Canopy Cover[5]		-0.233		0.367		-0.133		-0.433
Water Temperature	-0.083	-0.233	-0.250	-0.250	-0.300	-0.083	0.033	0.033
Dissolved Oxygen	0.083	-0.383	-0.567	-0.167	-0.100	0.000	0.150	-0.050
O_2 Saturation	-0.117	-0.383	-0.333	-0.167	-0.100	0.000	-0.033	-0.050
Chl *a*	0.092	0.967*	-0.251	$-0.650^\dagger$	0.360	0.100	0.452	0.833*
PH	-0.167	-0.233	-0.133	-0.167	-0.400	-0.300	-0.400	-0.333
Alkalinity	0.133	0.000	-0.567	-0.383	$-0.600^\dagger$	$-0.667^\dagger$	0.017	-0.183
Specific Conductance	0.167	0.017	-0.550	-0.300	$-0.650^\dagger$	$-0.667^\dagger$	-0.017	-0.250
NH_4-N	-0.267	0.217	0.150	-0.183	0.400	-0.167	-0.067	0.167
SRP	0.393	0.536	0.100	-0.192	0.285	0.176	0.301	0.544
TDP	-0.083	0.167	0.567	0.350	0.150	0.350	-0.250	0.133
Ca^{2+}	0.133	-0.083	-0.317	-0.150	$-0.633^\dagger$	-0.567	-0.067	-0.300
Mg^{2+}	0.350	0.067	-0.583	-0.533	$-0.667^\dagger$	-0.450	0.067	0.000
Na^+	0.150	0.217	-0.483	-0.550	-0.417	-0.250	0.117	0.283
K^+	0.117	0.200	0.083	-0.067	0.250	0.500	0.250	0.233
Cl^-	0.267	0.333	-0.400	-0.483	$-0.650^\dagger$	-0.550	0.000	0.133
SO_4^-	-0.200	-0.300	-0.083	0.017	-0.167	-0.533	-0.383	-0.567

[1] Total change in length over course of field study (length at metamorphosis – length at beginning of study).

[2] Number of days from beginning of field study until metamorphosis (stage 42, forelimb emergence).

[3] Survival from beginning of study until metamorphosis, adjusted to omit enclosures lost to predation at three sites).

[4] Length (mm) of tadpoles at stage 42, forelimb emergence.

[5] Canopy cover was only measured once during larval period.

Table 4.8
Correlations between habitat and water chemistry parameters and overall tadpole growth and development rates averaged over entire larval period. Values are Spearman Rank Correlation coefficients (r_s). Significance in indicated by asterisks ($^{*}p<0.05$ $^{\dagger}p<0.10$).

	Growth Rate[1]		Development Rate[2]	
	June	July	June	July
Canopy Cover[3]		-0.700*		-0.650†
Water Temperature	0.450	0.333	0.517	0.500
Dissolved Oxygen	0.367	0.200	0.617†	0.383
O_2 Saturation	0.267	0.200	0.467	0.383
Chl *a*	0.326	0.783*	0.209	0.617†
PH	-0.100	-0.033	0.167	0.233
Alkalinity	0.100	-0.150	0.467	0.250
Specific Conductance	0.067	-0.233	0.433	0.150
NH_4-N	-0.033	0.433	-0.133	0.250
SRP	0.059	0.310	-0.243	0.050
TDP	-0.183	-0.100	-0.533	-0.433
Ca^{2+}	-0.083	-0.383	0.200	-0.017
Mg^{2+}	0.283	0.167	0.517	0.500
Na^{+}	0.300	0.250	0.550	0.533
K^{+}	-0.067	-0.167	-0.217	-0.200
Cl^{-}	0.217	0.283	0.433	0.500
SO_4^{-}	-0.383	-0.467	-0.050	-0.100

[1] Mean daily growth (length) averaged over course of entire larval period (mm/day).
[2] Mean daily development (stage) averaged over course of entire larval period (stage/day).
[3] Canopy cover was only measured once during larval period.

Figure 4.1

Location of study sites in southwestern Michigan. All study sites were natural wetlands in Kalamazoo and Barry Counties.

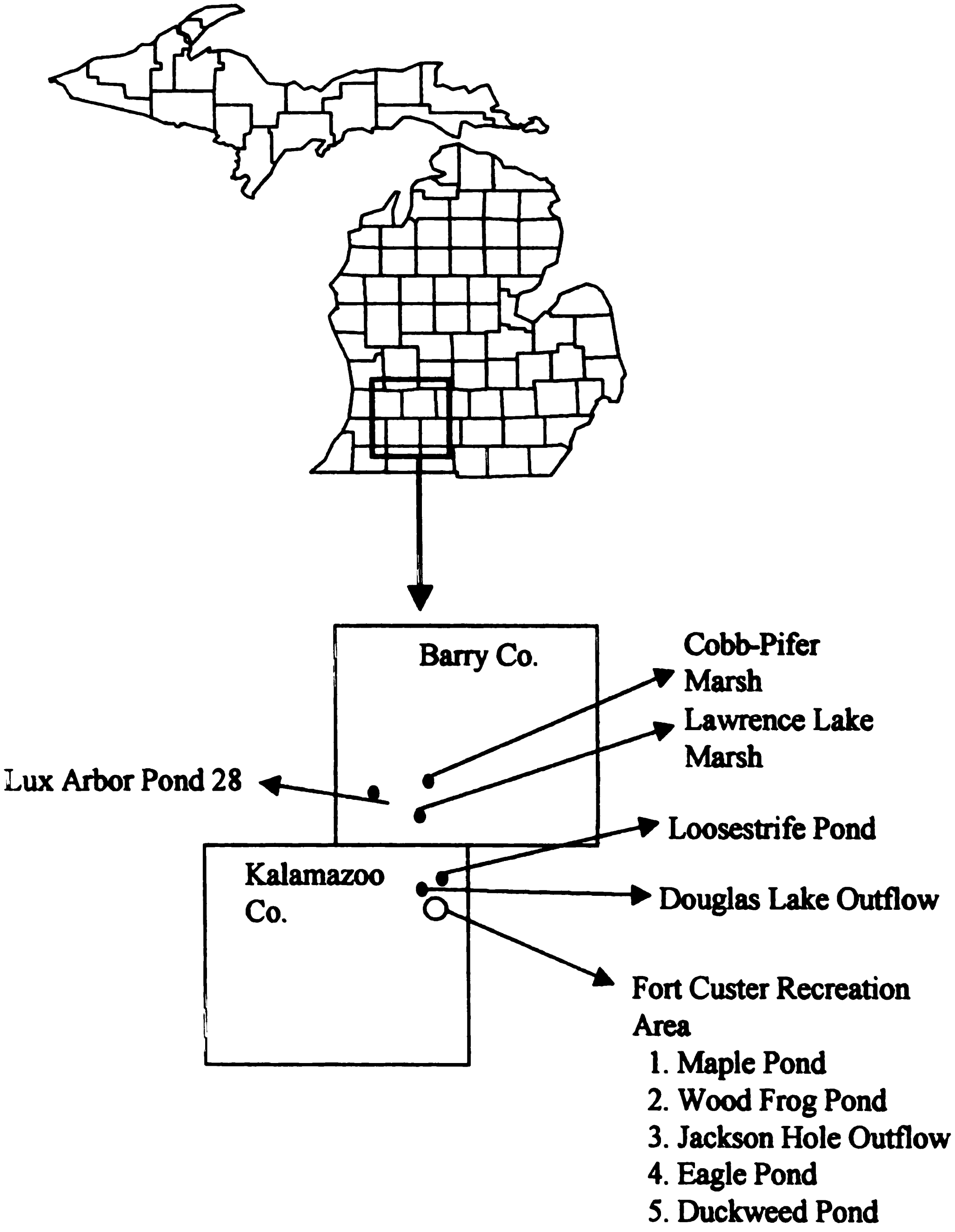


Figure 4.2

Mg^{2+} concentration and Specific Conductance of the 10 study sites. Both variables were used as an indicator of water source, with sites having higher Mg^{2+} concentrations and Specific Conductance more predominantly groundwater-fed, and site with lower values for both variables more precipitation-fed. Values plotted represent mean values of measurements taken monthly during the anuran breeding season (n=5) and their associated std. errors.

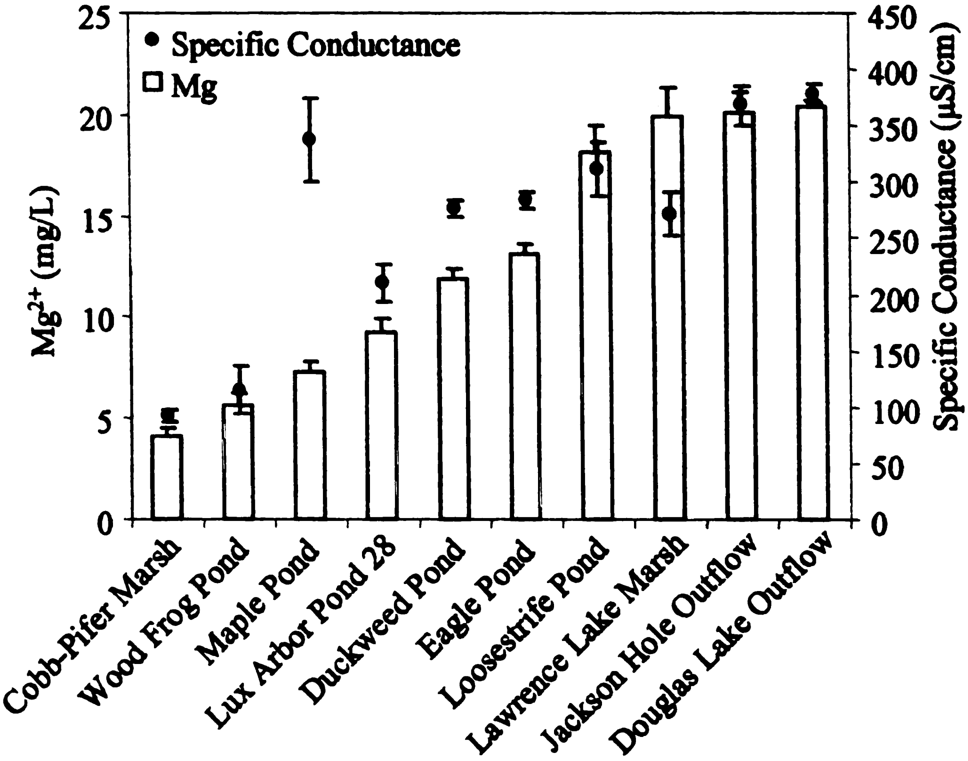


Figure 4.3

Relative abundance of invertebrates and fish sampled by bottle traps in 10 study sites. Predatory fish were present in 6 of the 10 sites, but comprised >5% of the total community in only one site (Eagle Pond). Species of predatory fish included Bluegill, Green sunfish, Pumpkinseed, and Largemouth bass.

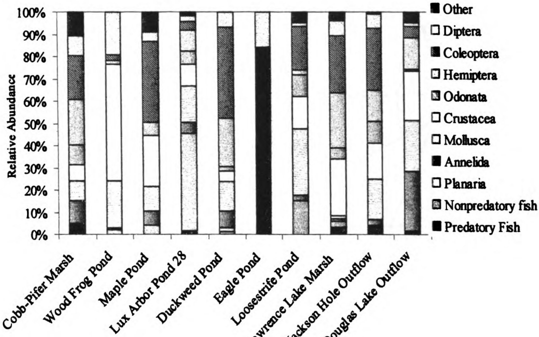


Figure 4.4

Growth rates of tadpoles at field study sites. Growth rates were measured at approximately weekly (5 – 8 days) intervals. Sites with open symbols are sites where mean water temperature was greater than 16°C; sites with darkened symbols had mean water temperatures less than 16°C.

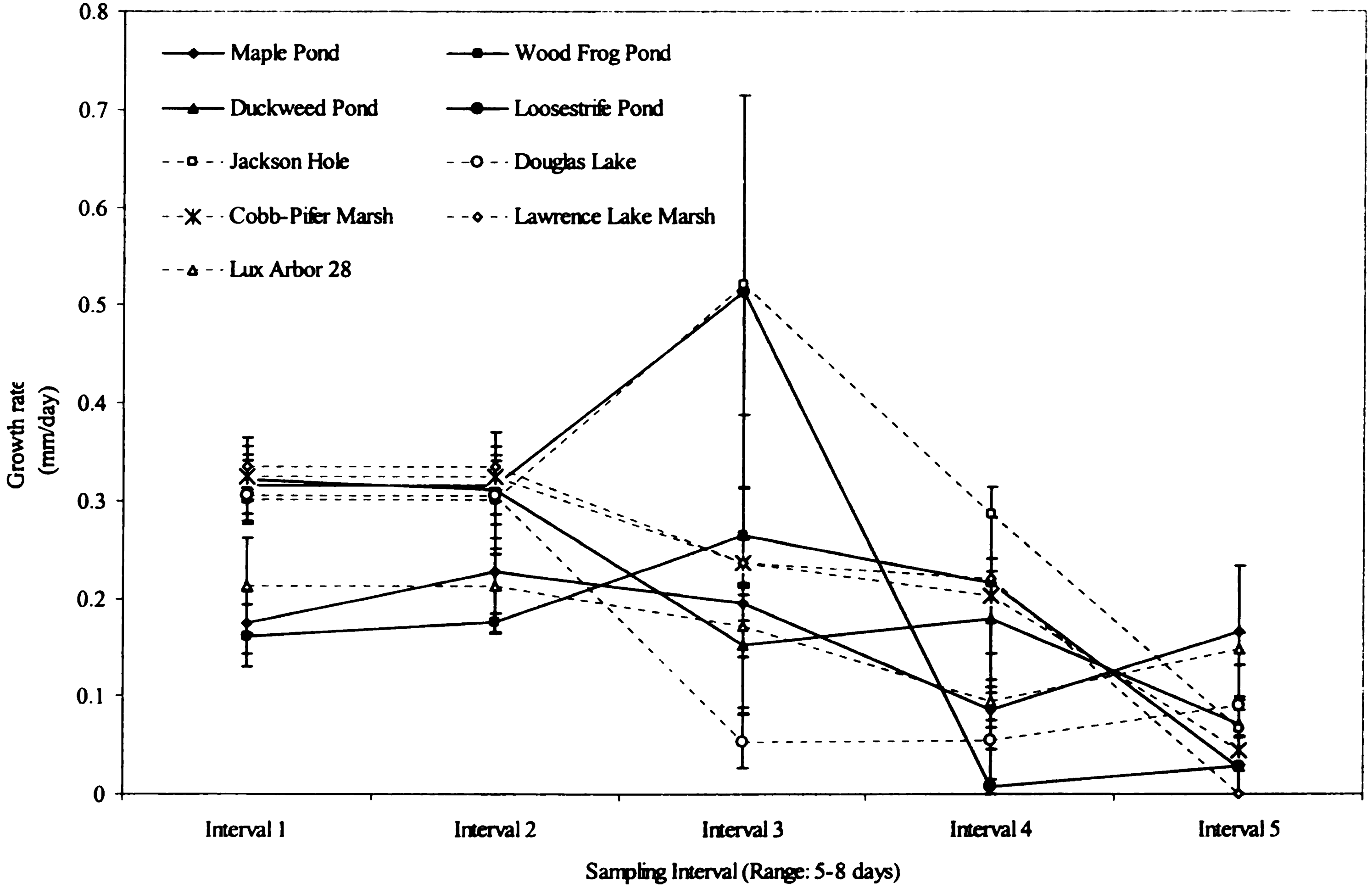


Figure 4.5

Growth Rate (mm/day) profiles of Spring peeper tadpoles over five weeks of field study related to (A) Pond permanence, (B) Canopy cover, and (C) Presence of fish predators.

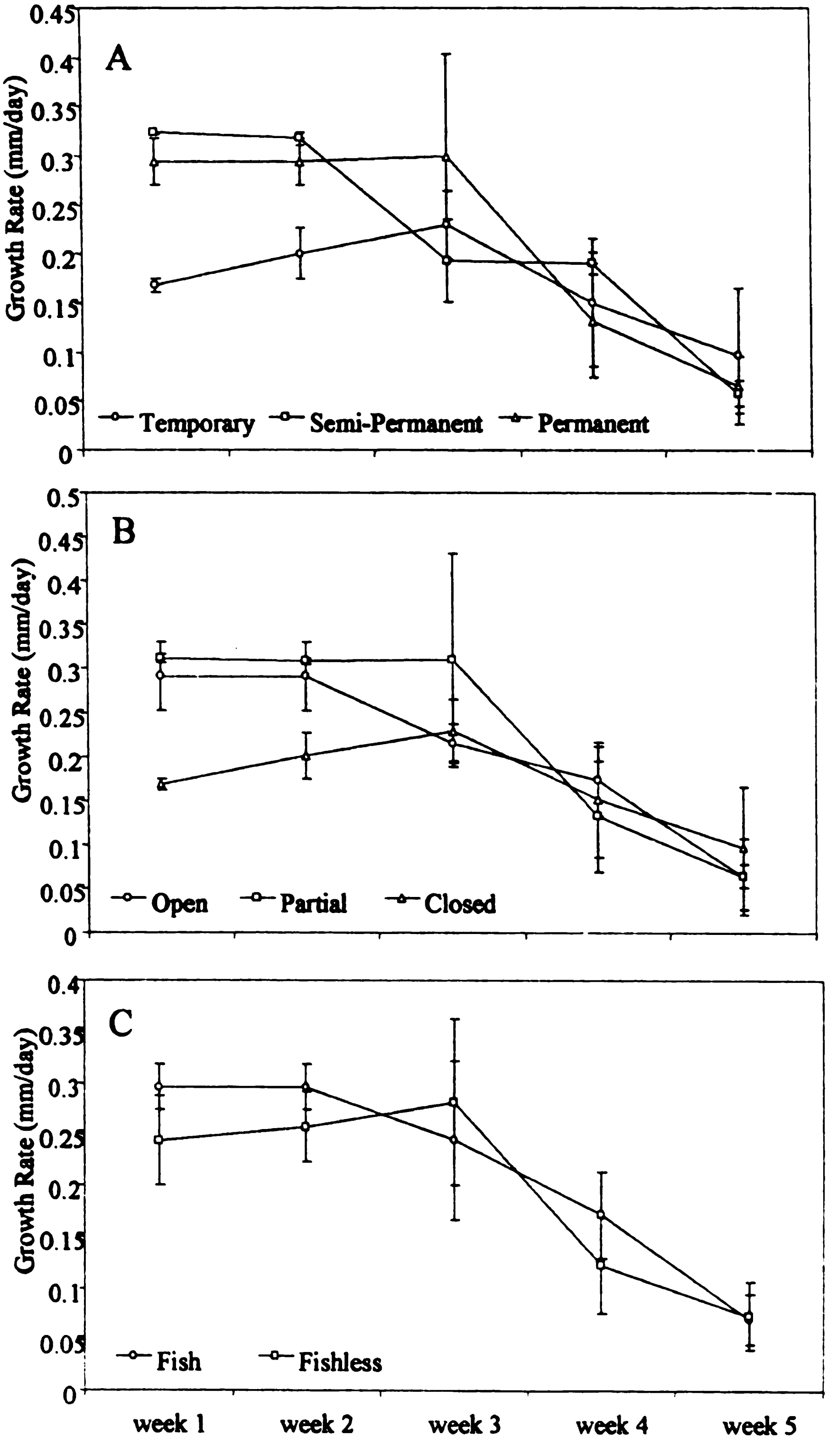
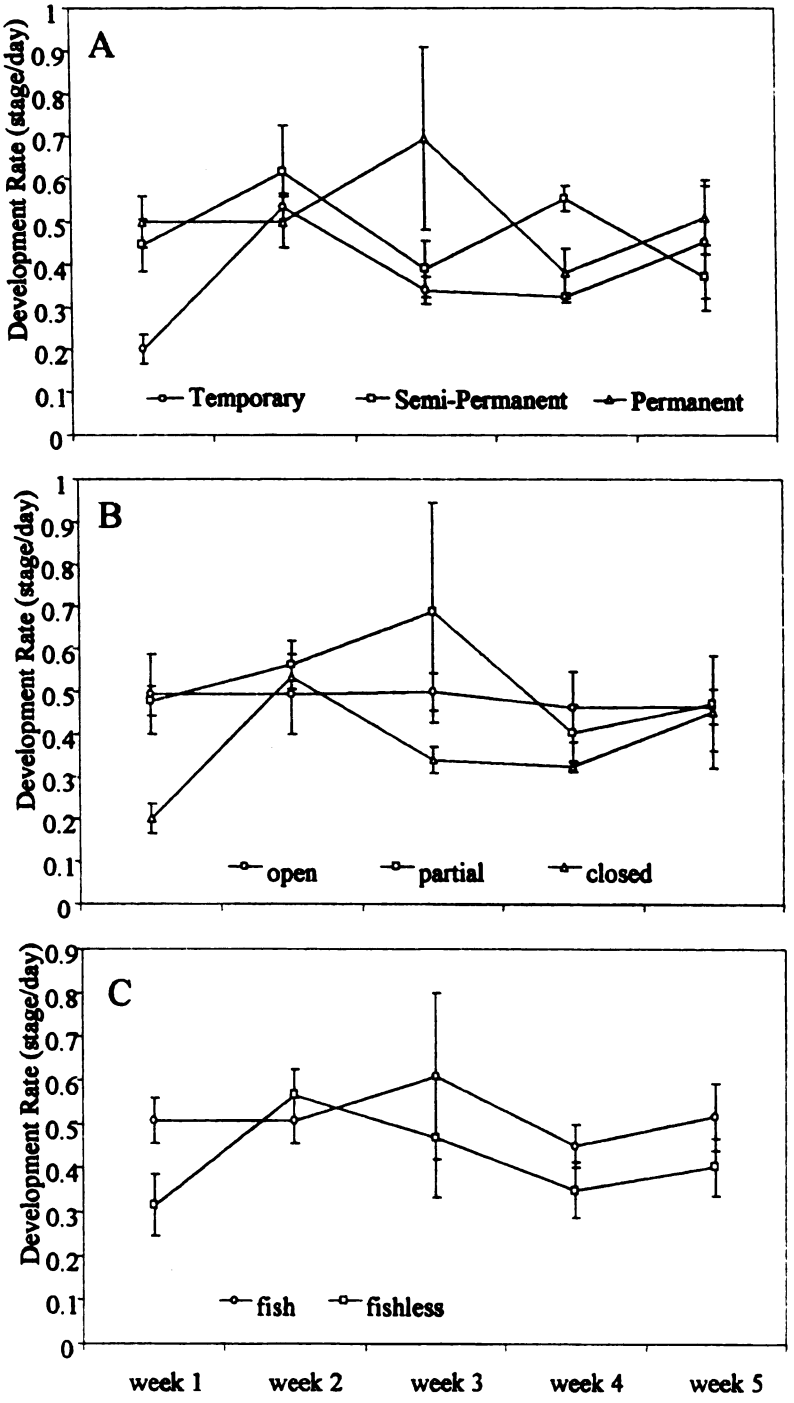


Figure 4.6

Development rate (stage/day) profiles of Spring peeper tadpoles over five weeks of field study related to (A) Pond permanence, (B) Canopy cover, and (C) Presence of fish predators.



Summary and Conclusions

Amphibians have been the focus of a surge of research activity since initial alarms were sounded in the early 1990s regarding declining amphibian populations worldwide. Even though specific causes for declines remain unknown, awareness of these organisms and their habits and habitats has been raised. With establishment of many state (e.g., MFTS), regional (e.g., Marsh Monitoring Program), and continent-wide (e.g., NAAMP) amphibian monitoring programs, annual data are being collected that will contribute to the understanding of species' distributions and trends in long-term population dynamics – provided data are collected continuously over several generations of the frog and toad species.

Michigan is home to 13 species of frogs and toads, with 12 occurring in the southern lower peninsula targeted in this study. I did not detect any major declines for any of these 12 species that warrant urgent or immediate remediation. However, these analyses represent only the first seven years of the Michigan Frog and Toad Survey data, essentially only a snapshot of long-term anuran population dynamics.

Site species richness fluctuated both among different wetland types and among years, but there were no consistent patterns. Only two species showed significant trends in site occupancy from 1996 to 2002; the proportion of sites occupied increased for *Rana catesbeiana* and decreased for *R. palustris*. Five species had significant trends in call index values over time, although these relationships explained little variance in linear regression models (Table 1.7). *Rana sylvatica, Hyla versicolor/chrysoscelis, Pseudacris crucifer,* and *R. clamitans* increased calling intensity over the seven years, while *Bufo* *americanus* decreased calling intensity. All statistically significant population trends for these species were small in magnitude and explained relatively little variance in the data. However, trends that were statistically significant should be further evaluated as MFTS data are accumulated annually to determine whether they are biologically significant for long-term population dynamics.

I used multiple analysis methods to evaluate population trends for several reasons. First, amphibian call surveys were based on protocols of the Breeding Bird Survey (BBS), and data analyses have been adapted from BBS methodology (Geissler and Sauer 1990). Second, the Wisconsin frog and toad survey has almost 20 years of data, and I used the methods developed by Mossman et al. (1998) for Wisconsin survey data to facilitate comparisons of population trends with those in neighboring states. Finally, until enough data have been gathered to evaluate changes in abundance and distribution over multiple generations of the longest-lived Michigan species (*R. catesbeiana*) and crucial empirical relationships relating calling intensity to actual population size have been developed, these data need to be evaluated using multiple approaches. If multiple methods indicate significant changes in distribution or abundance, then confidence in the results increases. Call surveys provide valuable information, but data must be analyzed and interpreted within the limitations of the survey methodology. These limitations include data reliability, inter-observer variation, dependence on volunteers for long-term data, subjective selection of survey routes, and poor understanding of how call index values are related to actual population size.

The limitations related to volunteers involved in the survey were addressed in Chapter Two. Volunteers were acceptably reliable in species identification, but were less so in assignment of call index values. Volunteer background and prior experience had little influence on data quality and consistency, which differs from the effects of observer experience seen in the BBS (Sauer et al. 1994, Kendall et al. 1996). These results indicate that the most robust analyses of population trends using MFTS data will use presence/absence (i.e., detection/non-detection) data, such as the site occupancy and route frequency regression methods I presented in the first chapter.

Volunteers are highly committed to the MFTS because of their interest in conserving native amphibians. Volunteers commit to collecting data on their route for a minimum of three years before establishing a new route (L.G. Sargent, personal communication), and active volunteers who participated in observer evaluation indicated that they intended to collect data for an average of 10 years. However, those who participated in the observer evaluation process may represent the most conscientious volunteers, and conclusions about data quality and commitment from volunteers who did not participate in the observer evaluation study remain unknown. Training materials and workshops offered by the MDNR are important to prepare volunteers for call surveys and will be continued given available funding.

Volunteer-based anuran call surveys have the potential to provide long-term data on anuran distribution and abundance over broad geographic scales. Amphibian populations, however, fluctuate dramatically under natural circumstances (e.g., Semlitsch et al. 1996, Alford and Richards 1999), and the challenge is to separate short-term patterns from long-term trends that are outside the natural wide range of variability. Shirose and Brooks (1997) suggested that amphibian monitoring programs should last at least as long as the generation time of the longest-lived species (up to 15 years for *Rana* *catesbeiana* in Michigan; Harding 1997). It is generally assumed that at least 10-15 years of data are needed from a monitoring program to identify patterns that are biologically meaningful at the population level (Mossman et al. 1998). The MFTS currently has eight years of data (seven of which are analyzed in the preceding chapters). However, this is still not long enough to identify population trends that are meaningful over the long run, as indicated by the relatively few and inconsistent patterns of distribution and abundance identified in Chapter One. The MFTS annually collects valuable data, and the value of this data as a contribution to regional management and conservation of amphibians increases as each year of data is added.

One of the most significant limitations of call survey data is the poor understanding of the empirical relationship between call index values and actual population size. This relationship actually needs to be addressed at several levels to fully understand how an index of the abundance of calling males is related to population parameters. The relationship between calling intensity (i.e., call index values) of breeding males and larval abundance should be evaluated to determine whether calling intensity of breeding males is a reliable predictor of successful reproduction. The relationship between larval abundance and the production of metamorphs needs to be determined to assess whether the often extremely high densities of tadpoles are reflected in numbers of juveniles dispersing into terrestrial habitats. The relationship between the numbers of metamorphs produced each season and the number that are subsequently recruited into the breeding adult population also needs to be determined. The sex ratio, which probably differs among species and among years (e.g., Green 1997a), also needs to be determined so that call index values of breeding males can be related to actual population size. Currently these empirical relationships are unknown, and assumptions regarding these issues are built into monitoring programs need to be addressed and tested. Data analyses such as those presented in the first three chapters will become more valuable once such relationships are empirically established.

Anurans respond to factors within habitats as well as at the landscape scale encompassing multiple habitats used during different portions of their life cycles. All of Michigan's anuran larvae are obligately aquatic. Habitat factors such as food availability, hydroperiod, canopy cover and predators affected tadpole performance in natural wetlands in southwestern Michigan, as reported in Chapter Four. Growth, development, and survival of *P. crucifer* tadpoles were highest at sites with intermediate hydroperiods, partial canopy cover, and few (if any) fish predators. More detailed manipulative experiments are needed to identify strongly influential factors in the larval habitat that are related to recruitment of adults to the breeding population.

Landscape factors, particularly land cover types, influenced the presence and abundance of anurans at wetland breeding sites, as discussed in Chapter Three. Generally, land cover types indicating habitat alteration or loss (i.e., roads, urban) negatively influenced presence and/or abundance of anurans while variables representing important foraging and breeding habitats (i.e., open land, wetlands) represented positive influences. Contrary to my expectations, no consistent negative associations with agricultural land were found in this study; agriculture both adjacent to wetland breeding sites and in the surrounding landscape was often positively associated with the presence and abundance of anurans. In this study, "agriculture" included all land that was intensively managed for vegetation production, including row crops, forage crops, orchards, vineyard, and nurseries. While row crops are probably quite inhospitable to anurans, the other types of agriculture may provide usable foraging habitat or dispersal corridors, or at least do not inhibit anuran presence or movement through these areas. Thus, future studies should separate agriculture into subunits (i.e., intensive row crops vs. other types of agricultural land uses) if crop rotations within the time frame of landscape and amphibian survey data allow.

Anuran presence was not more strongly related to factors at the 100 m buffer scale directly adjacent to survey sites than the 1000 m buffer scale representing their dispersal potential. Anuran abundance, on the other hand, was more strongly related to land cover variables at the larger 1000 m buffer scale. Anurans use a variety of habitats during their complex life cycles, and the overall species assemblage appears to benefit from a mosaic of habitat types in the landscape surrounding breeding sites within the distance most individuals are likely to disperse. Others have also indicated the importance of the landscape surrounding anuran breeding habitats for the management and conservation of these organisms (e.g., Hecnar and M'Closkey 1996, Semlitsch and Bodie 1998).

The associations I found between anuran presence and abundance and land cover variables provide valuable information for the management and conservation of these species. Population trends determined from large-scale monitoring programs (e.g., MFTS) can be combined with such habitat and landscape evaluations to obtain a more comprehensive understanding of the relationships of anurans to their potential habitats. In order to fully understand amphibian population dynamics and properly manage and conserve species and their habitats, we need to synthesize research evaluating influential factors at multiple scales (e.g., within habitat, landscape) for a variety of life history stages (e.g., larvae, juveniles, adults) over long time periods (at least 10 years).

APPENDIX

Appendix A

Survey questions presented to active volunteers on mail questionnaire. Responses were edited and evaluated as described in the text of Chapter Two.

---

1. When did you become involved with the Frog and Toad Survey (1996, 1997, 1998, 1999, 2000, 2001)?
2. How many years have you submitted data (1, 2, 3, 4, 5, 6)?
3. How many years do you anticipate submitting data?
4. How many years have you been involved with frogs, herps, or wildlife in general as an avid hobbyist or professional (0-5, 6-10, 11-15, 16-20, >20)?
5. With respect to the Frog and Toad Survey, please rate your current level of expertise at which you perceive yourself, on a scale from 1 (low) to 5 (high).
6. Please rate the level of expertise at which you perceived yourself before getting involved with the Michigan Frog and Toad Survey, on a scale from 1 (low) to 5 (high).
7. What forms of training did you participate in before beginning to survey your routes (Please mark all that apply) (attended training workshop, listened to training tape, practice in the field with a trained observer, other – specify)?
8. How many people participate in your survey runs each year?
9. Is this number consistent each year (yes, no)?
10. Do the same people participate in the survey each year (yes, no)?
11. Is there one person designated as the primary observer (yes, no)?
12. Are you the primary observer (yes, no)?

13. Please estimate the amount of time you spend listening at each site along your route, in minutes.

14. During the time of your involvement with this program, have there been discrepancies among observers in species heard or call indices that should be assigned (yes, no)?

15. If yes to previous question, please describe how these discrepancies are resolved in the space that follows.

16. Are you also an avid birder (yes, no)?

17. If yes, do you most often identify birds by sight, song, or both?

18. Are you involved in any additional wildlife monitoring programs (yes, no)?

19. If yes, please indicate which monitoring programs in which you participate (Marsh Monitoring Program, North American Breeding Bird Survey, Christmas Bird Count, Other – specify).

LITERATURE CITED

Literature Cited

Abramovitz, J.N. 1996. Imperiled waters, impoverished future: the decline of freshwater ecosystems. Paper 128. Worldwatch Institute, Washington, D.C.

Adams, M.J., K.O. Richter, and W.P. Leonard. 1997. Surveying and monitoring amphibians using aquatic funnel traps. Northwest Fauna 4: 47-54

Alford R.A. 1999. Ecology: resource use, competition, and predation. *In* R.W. McDiarmid, R.A. Altig. (eds.) Tadpoles: The Biology of Anuran Larvae, pp. 240-278. Univ. of Chicago Press, Chicago, IL USA.

Alford, R.A. and S.J. Richards. 1999. Global amphibian declines: a problem in applied ecology. Annual Review of Ecology and Systematics 30: 133-165

Altig, R., R.W. McDiarmid, K.A. Nichols, and P.C. Ustach. 1998. A key to the anuran tadpoles of the United States and Canada. Contemporary Herpetology Information Series. 1998 [Online] Available http://alpha.selu.edu/ch/chis/1998/2/index.htm)

Aminot A., Kirkwood D.S. & Kérouel R. 1997. Determination of ammonia in seawater by the indophenol-blue method: Evaluation of the ICES NUTS I/C 5 questionnaire. Mar. Chem. 56: 59-75

Ashley, E.P. and J.T. Robinson. 1996. Road mortality of amphibians, reptiles, and other wildlife on the Long Point Causeway, Lake Erie, Ontario. Canadian Field Naturalist 110: 403-412

Beebee, T.J.C. 1985. Discriminant analysis of amphibian habitat determinants in southeast England. Amphibia-Reptilia 6: 35-43

Beebee, T.J.C. 1995. Amphibian breeding and climate. Nature 374: 219-220

Berger, L., R. Speare, P. Daszak, D.E. Green, and A.A. Cunningham, C.L. Goggin, R. Slocombe, M.A. Ragan, A.D. Hyatt, K.R. McDonald, H.B. Hines, K.R. Lips, G. Marantelli, and H. Parkes. 1998. Chytriodiomycosis causes amphibian mortality associated with population declines in the rain forests of Australia and Central America. Proceedings of the National Academy of Sciences, USA. 95: 9031-9036

Bertram, S. and M. Berrill. 1997. Fluctuations in a northern population of gray treefrogs, *Hyla versicolor*. Herpetological Conservation 1: 57-63

Berven, K.A. 1990. Factors affecting population fluctuations in larval and adult stages of the wood frog (*Rana sylvatica*). Ecology 71(4): 1599-1608

Berven, K.A. and T.A. Grudzien. 1990. Dispersal in the wood frog (*Rana sylvatica*): implications for genetic population structure. Evolution 44: 2047-2056

Bishop, C.A. 1992. The effects of pesticides on amphibians and the implications for determining causes of declines in amphibian populations. Pp. 67-70 *In:* C.A. Bishop and K.E. Pettitt (eds.). Declines in Canadian Amphibian Populations: Designing a National Monitoring Strategy. Occasional Paper No. 76. Canadian Wildlife Service, Ottawa, ON, Canada

Bishop, C.A., K.E. Pettit, M.E. Gartshore, and D.A. Macleod. 1997. Extensive monitoring of anuran populations using call counts and road transects in Ontario (1992-1993). Herpetological Conservation 1: 149-160

Blaustein, A.R., and D.B. Wake. 1990. Declining amphibian populations: a global phenomenon? Trends in Ecology and Evolution 5:203-204.

Blaustein, A.R., D.B. Wake, and W.P. Sousa. 1994a. Amphibian declines: judging stability, persistence, and susceptibility of populations to local and global extinctions. Conservation Biology 8: 60-71

Blaustein, A.R., P.D. Hoffman, D.G. Hokit, J.M. Kiesecker, S.D. Walls, and J.B. Hays. 1994b. UV repair and resistance to solar UV-B in amphibian eggs: a link to population declines? Proceedings of the National Academy of Sciences, USA 91: 1791-1795

Blaustein, A.R., J.M. Kiesecker, D.P. Chivers, and R.G. Anthony. 1997. Ambient UV-B radiation causes deformities in amphibian embryos. Proceedings of the National Academy of Sciences, USA. 94: 13735-13737

Bonin, J., J. DesGranges, J. Rodrigue, and M. Ouellet. 1997. Anuran species richness in agricultural landscapes of Québec: forseeing long-term results of road call surveys. Herpetological Conservation 1: 141-149

Bowers , D.G., D.E. Andersen, and N.H. Euliss, Jr. 1998. Anurans as indicators of wetland condition in the prairie pothole region of North Dakota: an environmental monitoring and assessment program pilot project. Pp. 369-378 *in:* M. J. Lannoo, editor. Status and Conservation of Midwestern Amphibians. University of Iowa, Iowa City, Iowa, USA

Bradford, D.F. 1989. Allotopic distributions of native frogs and introduced fishes in high Sierra Nevada lakes of California: implications of the negative effect of fish introductions. Copeia 1989: 775-778

Bradford, D.F., F. Tabatabai, and D.M. Graber. 1993. Isolation of remaining populations of the native frog, *Rana muscosa*, by introduced fishes in the Sequoia and Kings Canyon National Parks, California. Conservation Biology 7: 882-888

Breden, F. 1988. The natural history and ecology of Fowler's toad, *Bufo woodhousei fowleri* (Amphibia: Bufonidae) in the Indiana Dunes National Lakeshore. Fieldiana Zoology 49: 1-16

Brodman, R. and M. Kilmurry. 1998. Status of amphibians in Northwestern Indiana. Pp. 125-136 *in:* M. J. Lannoo, editor. Status and Conservation of Midwestern Amphibians. University of Iowa, Iowa City, Iowa, USA

Brown, J.H., and A. Kodric-Brown. 1977. Turnover rates in insular biogeography: effect of immigration on extinction. Ecology 58: 445-449

Bunnell, J.F. and R.A. Zampella. 1999. Acid water anuran pond communities along a regional forest to agro-urban ecotone. Copeia 1999: 614-662

Burton, T.M. and G.E. Likens. 1975. Salamander populations and biomass in the Hubbard Brook Experimental Forest, New Hampshire. Copeia 1975: 541-546

Cantrell, K.J., S.M. Serkiz and E.M. Perdue. 1990. Evaluation of acid neutralizing capacity data for solutions containing natural organic acids. Geochim Cosmochim Acta 54: 1247-1254.

Carey, C. and C.J. Bryant. 1995. Possible interrelationships among environmental toxicants, amphibian development, and decline of amphibian populations. Environmental Health Perspectives. 103 (Supp. 4): 13-17

Carey, C. and M.A. Alexander. 2003. Climate change and amphibian declines: is there a link? Diversity and Distributions. 9: 111-121

Carr, L.W. and L. Farhig. 2001. Effect of road traffic on two amphibian species of differing vagility. Conservation Biology 15: 1071-1078

Casper, G.S. 1998. Review of the status of Wisconsin amphibians. Pp. 199-205 *in:* M. J. Lannoo, editor. Status and Conservation of Midwestern Amphibians. University of Iowa, Iowa City, Iowa, USA

Collins, J.P. 1979. Intrapopulation variation in the body size at metamorphosis and timing of metamorphosis in the bullfrog, *Rana catesbeiana.* Ecology 60: 738-749

Comer, P.J. 1996. Wetland trends in Michigan since 1800: a preliminary assessment. Report to the U.S. E.P.A. and Land and Water Division, Michigan Department of Environmental Quality, Michigan Natural Features Inventory, Lansing, MI

Conant, R. and J.T. Collins. 1998. A field guide to reptiles and amphibians of eastern and central North America. 3rd ed. (expanded). Houghton Mufflin co. New York, NY

Crouch, W.B. 1999. Evaluation of the North American Amphibian Monitoring Program's (NAAMP) calling anuran survey. M.S. Thesis. University of Rhode Island, Kingston, RI

Crouch, W.B. and P.W.C. Paton. 2002. Assessing the use of call surveys to monitor breeding anurans in Rhode Island. Journal of Herpetology 36: 185-192.

Crump, M.L. 1989. Effect of habitat drying on developmental time and size at metamorphosis in *Hyla pseudopuma*. Copeia 1989: 794-797

Crump, M. L., and N. J. Scott, Jr. 1994. Standard techniques for inventory and monitoring--visual encounter surveys. Pages 84 - 92 in W. R. Heyer, M. A. Donnelly, R. W. McDiarmid, L. C. Hayek, and M. S. Foster, editors. Measuring and monitoring biological diversity: standard methods for amphibians. Smithsonian Institution Press, Washington, D.C.

Dahl, T.E. 2000. Status and trends of wetlands in the conterminous United States 1986 to 1997. U.S. Department of the Interior, Fish and Wildlife Service. Washington, D.C. 82 pp.

Daigle, C. 1997. Distribution and abundance of the chorus frog *Pseudacris triseriata* in Québec. Herpetological Conservation 1: 73-77

DeGraaf, R.M. and D.D. Rudis. 1990. Herpetofaunal species composition and relative abundance among three New England forest types. Forest Ecology and Management 32: 155-165

Delis, P.R., H.R. Mushinsky, and E.D. McCoy. 1996. Decline of some west-central Florida anuran populations in response to habitat degradation. Biodiversity and Conservation 5: 1579-1595

Detenbeck, N.E., S.M. Galatowitsch, J. Atkinson, and H. Ball. 1999. Evaluating perturbations and developing restoration strategies for inland wetlands in the Great Lakes Basin. Wetlands 19: 789-820

Driscoll, D. 1998. Counts of calling males as estimates of population size in the endangered frogs *Geocrinia alba* and *G. vitellina*. Journal of Herpetology 32: 475-481

Duellman, W.E. and L. Trueb. 1986. Biology of Amphibians. Johns Hopkins University Press, Baltimore, MD

Dunson, W.A. and J. Connell. 1982. Specific inhibition of hatching in amphibian embryos by low pH. J. Herp. 16: 314-316

Dunson, W.A. and J. Travis. 1991. The role of abiotic factors in community organization. American Naturalist 138: 1067-1091

Erskine, A. J. 1978. The first ten years of the cooperative Breeding Bird Survey in Canada. Canadian Wildlife Service Report Series No. 42, Hull, Quebec, Canada

Fahrig, L. 1997. Relative effects of habitat loss and fragmentation on population extinction. Journal of Wildlife Management 61: 603-610

Fahrig, L., J.H. Pedlar, S.E. Pope, P.D. Taylor, and J.F. Wegner. 1995. Effect of road traffic on amphibian density. Biological Conservation 74: 177-182

Findlay, C.S. and J. Houlahan. 1997. Anthropogenic correlates of species richness in southeastern Ontario wetlands. Conservation Biology 11: 1000-1009

Fisher, R.N. and H.B. Shaffer. 1996. The decline of amphibians in California's Great Central Valley. Conservation Biology 10: 1387-1397

Forman, R.T.T. and L.E. Alexander. 1998. Roads and their major ecological effects. Annual Review of Ecology and Systematics 29: 207-231

Freda, J. and W.A. Dunson. 1986. Effects of low pH and other chemical variables on the local distribution of amphibians. Copeia 1986: 454-466

Freda, J., W.J. Sadinski, and W.A. Dunson. 1991. Long term monitoring of amphibian populations with respect to acidic deposition. Water, Air, and Soil Pollution 55: 445-462

Geissler, P.H. and J.R. Sauer. 1990. Topics in route-regression analysis. Pp. 54-57 *In:* J.R. Sauer and S. Droege (eds.). Survey designs and statistical methods for the estimation of avian population trends. U.S. Fish and Wildlife Service, Biological Report 90(1)

Genet, K.S. and L.G. Sargent. 2003. Evaluation of methods and data quality from a volunteer-based amphibian call survey. Wildlife Society Bulletin 31: *in press*

Gerhardt, H.C., M.B. Ptacek, L. Barnett, and K.G. Torke. 1994. Hybridization in the diploid-tetraploid treefrogs *Hyla chrysoscelis* and *Hylca versicolor.* Copeia 1994: 51-59

Gibbs, J.P. 1993. Importance of small wetlands for the persistence of local populations of wetland associated animals. Wetlands 13: 25-31

Gibbs, J.P. and A.R. Breisch. 2001. Climate warming and calling phenology of frogs near Ithaca, New York, 1900-1999. Conservation Biology 15: 1175-1178

Gosner, K.L. 1960. A simplified table for staging anuran embryos and larvae with notes on identification. Herpetologica 16: 183-190

Green, D.M. 1997a. Temporal variation in abundance and age structure in Fowler's Toads, *Bufo fowleri,* at Long Point, Ontario. Herpetological Conservation 1: 45-56.

Green, D. M. 1997b. Perspectives on amphibian population declines: defining the problem and searching for answers. Herpetological Conservation 1: 291-308

Griffiths, R.A. 1985. A simple funnel trap for studying newt populations and an evaluation of trap behavior in smooth and palmate newts *Triturus vulgaris* and *T. helviticus*. Herpetological Journal 1: 5-9

Guerry, A.D. and M.L. Hunter, Jr. 2002. Amphibian distributions in a landscape of forests and agriculture: an examination of landscape composition and configuration. Conservation Biology 16: 745-754

Halley, J.M., R.S. Oldham, and J.W. Arntzen. 1996. Predicting the persistence of amphibian populations with the help of a spatial model. Journal of Applied Ecology 33: 455-470

Harding, J.H. 1997. Amphibians and reptiles of the Great Lakes region. University of Michigan Press. Ann Arbor, MI

Harkey, G.A. and R.D. Semlitsch. 1988. Effects of temperature on growth, development, and color polymorphism in the ornate chorus frog, *Pseudacris ornata*. Copeia 1988: 1001-1007

Harris, R.N. 1999. The anuran tadpole: evolution and maintenance. Pp. 279-294 *In* R.W. McDiarmid, R.A. Altig. (eds.) Tadpoles: The Biology of Anuran Larvae, Univ. of Chicago Press, Chicago, IL USA.

Hay, R. 1998. Blanchard's cricket frogs in Wisconsis: a status report. Pp. 79-82 *in:* M. J. Lannoo, editor. Status and Conservation of Midwestern Amphibians. University of Iowa, Iowa City, Iowa, USA

Hayes, M.P. and M.R. Jennings. 1986. Decline of frog species in western North America: are bullfrogs (*Rana catesbeiana*) responsible? Journal of Herpetology 20: 490-509

Hecnar, S. J. 1997. Amphibian pond communities in southwestern Ontario. Herpetological Conservation. 1: 1-15

Hecnar, S.J and R.T. M'Closkey. 1996. Regional dynamics and the status of amphibians. Ecology 77: 2091-2097

Hecnar, S.J. and R.T. M'Closkey. 1997a. The effects of predatory fish on amphibian species richness and distribution. Biological Conservation 79: 123-131

Hecnar, S.J. and R.T. M'Closkey. 1997b. Spatial scale and determination of species status of the green frog. Conservation Biology 11: 670-682

Hecnar, S.J. and R.T. M'Closkey. 1998. Species richness patterns of amphibians in southwestern Ontario ponds. Journal of Biogeography 25: 763-772

Hemesath, L. M. 1998. Iowa's frog and toad survey, 1991-1994. Pages 206-216 *in:* M. J. Lannoo, editor. Status and Conservation of Midwestern Amphibians. University of Iowa, Iowa City, Iowa, USA

Hine , R.L., B.L. Les, and B.F. Hellmich. 1981. Leopard frog populations and mortality in Wisconsin, 1974-1976. Technical Bulletin No. 122, Wisconsin Dept. of Natural Resources, Madison, WI

Hollands, G.G. 1987. Hydrogeologic classification of wetlands in glaciated regions. National Wetlands Newsletter 9: 6-9

Horne, M. T. and W. A. Dunson. 1995. Effects of low pH, metals, and water hardness on larval amphibians. Archives of Environmental Contamination and Toxicology. 29:500-505.

Houlahan, J.E., C.S. Finlay, B.R. Schmidt, A.H. Meyer, and S.L. Kuzmin. 2000. Quantitative evidence for global amphibian population declines. Nature 404: 752-755

Huff, J. 1991. Frog and toad survey 1991. Madison: Wisconsin Department of Natural Resources. Technical Report. pp. 114-123

Hunter, M.L., Jr., A.J.K. Calhoun, and M. McCullough. 1999. Maine Amphibians and Reptiles. University of Maine Press, Orono, ME USA

Johnson, B. 1992. Habitat loss and declining amphibian populations. Pp. 71-75 *In:* C.A. Bishop and K.E. Pettit (eds.) Declines in Canadian Amphibian Populations: Designing a National Monitoring Strategy. Occasional Paper No. 76. Canadian Wildlife Service

Jongman, R.H.G., C.J.F. ter Braak, and O.F.R. van Tongeren (eds.). 1995. Data Analysis in Community and Landscape Ecology. Cambridge University Press, Cambridge, England

Kats, L.B., J.W. Petranka, and A. Sih. 1988. Antipredator defenses and the persistence of amphibian larvae with fishes. Ecology 69: 1865-1870

Kendall, W. L., B.G. Peterjohn, and J.R. Sauer. 1996. First-time observer effects in the North American Breeding Bird Survey. The Auk 113: 823-829

Kiesecker, J.M. and A.R. Blaustein. 1997. Population differences in responses to red-legged frogs (*Rana aurora*) to introduced bullfrogs. Ecology 78: 1752-1760

Kiesecker, J.M, A.R. Blaustein, and L.K. Belden. 2001. Complex causes of amphibian population declines. Nature 410: 681-684

Kiffney, P.M. and J.S. Richardson. 2001. Interactions among nutrients, periphyton, and invertebrate and vertebrate (Ascaphus truei) grazers in experimental channels. Copeia 2001: 422-429

Kline, J. 1998. Monitoring amphibians in created and restored wetlands. Pages 360-368 *in:* M. J. Lannoo, editor. Status and Conservation of Midwestern Amphibians. University of Iowa, Iowa City, Iowa, USA

Knutson, M.G., J.R. Sauer, D.A. Olsen, M.J. Mossman, L.M. Hemesath, and M.J. Lannoo. 1999. Effects of landscape composition and wetland fragmentation on frog and toad abundance and species richness in Iowa and Wisconsin, U.S.A. Conservation Biology 13: 1437-1446

Knutson, M.G., J.R. Sauer, D.A. Olsen, M.J. Mossman, L.M. Hemesath, and M.J. Lannoo. 2000. Landscape associations of frog and toad species in Iowa and Wisconsin, USA. Journal of the Iowa Academy of Science 107: 134-145

Koloszvary, M.B., and R.K. Swihart. 1999. Habitat fragmentation and the distribution of amphibians: patch and landscape correlates in farmland. Canadian Journal of Zoology 77: 1288-1299

Kupferberg, S.J. 1997. The role of larval diet in anuran metamorphosis. American Zoologist 37: 146-159

Kupferberg, S.J., J.C. Marks, and M.E. Power. 1994. Effects of variation in natural algal and detrital diets on larval anuran (*Hyla regilla*) life history traits. Copeia 1994: 446-457

Laan, R. and B. Verboom. 1990. Effects of pool size and isolation on amphibian communities. Biological Conservation 54: 251-262

Lannoo, M.J., K. Lang, T. Waltz, and G.S. Phillips. 1994. An altered amphibian assemblage: Dickinson County, Iowa, 70 years after Frank Blanchard's survey. American Midland Naturalist 131(2):311-319

Lannoo, M.J. 1998. Status and Conservation of Midwestern Amphibians. University of Iowa, Iowa City, Iowa, USA

Lee, Y. M. 1998. Final report on Blanchard's cricket frog (*Acris crepitans blanchardi*) surveys in southern Michigan. A report to the U.S. Environmental Protection Agency, EPA wetland enhancement grant and critical small non-contiguous wetlands project and Michigan Dept. of Natural Resources, Parks and Recreation Division. Michigan Natural Features Inventory report no. 1998-03. 13 pp. + appendices.

Lehtinen, R.M., S.M. Galatowitsch, and J.R. Tester. 1999. Consequences of habitat loss and fragmentation for wetland amphibian assemblages. Wetlands 19: 1-12

Lehtinen, R. M. 2001. Surveys for three rare amphibians in southeastern Michigan: Blanchard's cricket frog (*Acris crepitans lanchardi*), the four toed salamander (*Hemidactylium scutatum*), and the smallmouth salamander (*Ambystoma texanum*). Final report to the Michigan Dept. of Natural Resources, August 2001. 18 pp. + appendices.

Lepage, M., R. Courtois, and C. Daigle. 1997. Surveying calling anurans in Quebec using volunteers. Herpetological Conservation 1: 128-140

Lepczyk, C.A. 2002. Effects of human activities on birds across landscapes in the Midwest. Ph.D. Dissertation. Dept. of Fisheries and Wildlife, Michigan State University

Licht, L.E. and K.P. Grant. 1997. The effects of ultraviolet radiation on the biology of amphibians. American Zoologist 37: 137-145

Link, W.A. and J.R. Sauer. 1994. Estimating equations estimates of trends. Bird Populations 2:23-32

Link, W.A., and Sauer, J.R. 1997. Estimation of population trajectories from count data. Biometrics 53(2), 488-497.

Lips, K.R. 1998. Decline of a tropical montane amphibian fauna. Conservation Biology 12: 106-117

Loman, J. 2002. *Rana temporaria* metamorph production and population dynamics in the field: effects of tadpole density, predation, and pond drying. Journal for Nature Conservation. 10: 95-107

Lucas, E.A. and W.A. Reynolds. 1967. Temperature selection by amphibian larvae. Physiol. Zool. 40: 159-171

Lynch, J.A., G.B. Rishel, and E.S. Corbett. 1984. Thermal alteration of streams draining clearcut watersheds: quantification and biological implications. Hydrobiologia 111: 161-169

Mader, H.J. 1984. Animal habitat isolation by roads and agricultural fields. Biological Conservation 29: 81-96

Maxwell, S.E. and H.D. Delaney. 1990. Designing experiments and analyzing data: a model comparison perspective. Wadsworth, Belmont, CA

Merrell, D.J. 1977. Life history of the leopard frog, *Rana pipiens*, in Minnesota. Occasional Paper Number 15. Bell Museum of Natural History. University of Minnesota, Minneapolis, MN, USA

Mierzwa, K.S. 1998. Status of Northeastern Illinois amphibians. Pp. 115-124 *in:* M. J. Lannoo, editor. Status and Conservation of Midwestern Amphibians. University of Iowa, Iowa City, Iowa, USA

Miller, R. G. 1981. Simultaneous statistical inference, 2nd ed. Springer Verlag, Berlin

Mitchell, J.C., S.C. Rinehart, J.F. Pagels, K.A. Buhlmann, and C.A. Pague. 1997. Factors influencing amphibian and small mammal assemblages in central Appalachian forests. Forest Ecology and Management 96: 65-76

Moriarty, J.J. 1998. Status of amphibians in Minnesota. Pp. 166-168 *in:* M. J. Lannoo, editor. Status and Conservation of Midwestern Amphibians. University of Iowa, Iowa City, Iowa, USA

Morin, P. J. 1983. Predation, competition, and the composition of larval anuran guilds. Ecological Monographs 53: 119-138

Morrison, D.F. 1990. Multivariate statistical methods (3rd ed.). McGraw Hill. New York, NY USA

Mossman, M.J. and R.L. Hine. 1984. The Wisconsin frog and toad survey: establishing a long-term monitoring program. Endangered Resources Report No. 9. Wisconsin Dept. of Natural Resources, Madison, WI

Mossman, M. J., L. M. Hartman, R. Hay, J. R. Sauer, and B. J. Dhuey. 1998. Monitoring long-term trends in Wisconsin frog and toad populations. Pages 169-198 *in:* M.J. Lannoo, editor. Status and Conservation of Midwestern Amphibians. University of Iowa, Iowa City, Iowa, USA

Moyle, P.B. and R.A. Leidy. 1992. Loss of biodiversity in ecosystems: evidence from fish faunas. Pp. 127-169 in P.L. Fiedler and S.K. Jain (eds.). Conservation biology: the theory and practice of nature conservation, preservation, and management. Chapman and Hall. New York, NY

Muths, E., P.S. Corn, A.P. Pessier, and D.E. Green. Evidence for disease-related amphibian declines in Colorado. Biological Conservation 110: 357-365

O'Brien, R.G. and M.K. Kaiser. 1985. MANOVA method for analyzing repeated measures designs: an extensive primer. Psychological Bulletin 97: 316-333

Pais, R.C., S.A. Bonney, and W.C. McComb. 1988. Herpetofaunal species richness and habitat associations in an eastern Kentucky forest. Proceedings of the Annual Conference of Southeastern Associations of Fish and Wildlife Agencies 42: 448-455

Pandian, T.J. and M.P. Marian. 1985. Predicting anuran metamorphosis and energetics. Physiol. Zool. 58: 538-552

Patterson, J.W. and A.J. McLachlan. 1989. Larval habitat duration and size at metamorphosis in frogs. Hydrobiologia 171: 121-126

Pechmann, J.H.K., D.E. Scott, R.D. Semlitsch, J.P. Caldwell, L.J. Vitt, and J.W. Gibbons. 1991. Declining amphibian populations: the problem of separating human impacts from natural fluctuations. Science 253: 892-895

Pechmann, J.H.K. and H.M. Wilbur. 1994. Putting declining amphibian populations in perspective: natural fluctuations and human impacts. Herpetologica 50: 65-84

Pentecost, E.D. and R.C. Vogt. 1976. Amphibians and reptiles of the Lake Michigan drainage basin. Environmental Status of the Lake Michigan Region, Vol. 16. Argonne National Laboratory, Argonne, IL

Peterjohn , B.G., J.R. Sauer, and W.A. Link. 1994. The 1992 and 1993 summary of the North American Breeding Bird Survey. Bird Populations 2: 46-51

Pope, S.E., L. Fahrig, and H.G. Merriam. 2000. Landscape complementation and metapopulation effects on leopard frog populations. Ecology 81: 2498-2508

Pounds, J.A. and M.L. Crump. 1994. Amphibian declines and climate disturbance: the case of the golden toad and the harlequin frog. Conservation Biology 8: 72-85

Power, T., K.L. Clark, A. Harnfeist, and D.B. Peakall. 1989. A review and evaluation of the amphibian toxicological literature. Technical Report No. 61. Canadian Wildlife Service, Ottawa, ON, Canada

Reh, W. and A. Seitz. 1990. The influence of land use on the genetic structure of populations of the common frog, *Rana temporaria*. Biological Conservation 54: 239-249

Richards, S.J., K.R. McDonald, and R.A. Alford. 1993. Declines in populations of Australia's endemic tropical rainforest frogs. Pacific Conservation Biology 1: 66-77

Richter, K.O. 1995. A simple aquatic funnel trap and its application to wetland amphibian monitoring. Herpetological Review 26: 90-91

Robbins, C.S., D. Bystrak, and P.H. Geissler. 1986. The Breeding Bird Survey: its first fifteen years, 1965-1979. U.S. Fish and Wildlife Service, Resource Publication 157

Rosenberg, E.A. and B.A. Pierce. 1995. Effect of initial mass on growth and mortality at low pH in tadpoles of *Pseudacris clarkii* and *Bufo valliceps*. J. Herp. 29: 181-185

Rowe, C.L. and W.A. Dunson. 1995. Impacts of hydroperiod on growth and survival of larval amphibians in temporary ponds of central Pennsylvania. Oecologia 102: 397-403

Saber, P.A. and W.A. Dunson. 1978. Toxicity of bog water to embryonic and larval anuran amphibians. J. Exp. Biol. 204: 33-42

Sargent, L. G. 2000. Frog and toad population monitoring in Michigan. Journal of the Iowa Academy of Sciences 107: 195-199

Sarkar, S. 1996. Ecological theory and anuran declines. BioScience 46: 199-207

Sauer, J. R., B. G. Peterjohn, and W. A. Link. 1994. Observer differences in the North American Breeding Bird Survey. Auk 111:50-62.

Saunders, D.L., J.J. Weeuwig, and A.C.J. Vincent. 2002. Freshwater protected areas: strategies for conservation. Conservation Biology 16: 30-41

Scott, N. J., Jr. and B. D. Woodward. 1994. Surveys at breeding sites. Pages 118-125 *in:* W.R. Heyer, M.A. Donnelly, R.W. McDiarmid, L.C. Hayek, and M.S. Foster, editors. Measuring and monitoring biological diversity: standard methods for amphibians. Smithsonian. Washington, D.C., USA

Semlitsch, R.D. 2000. Principles for management of aquatic-breeding amphibians. Journal of Wildlife Management 64: 615-631

Semlitsch, R.D. 2002. Critical elements for biologically-based recovery plans of aquatic-breeding amphibians. Conservation Biology 16: 619-629

Semlitsch, R.D., D.E. Scott, J.H.K. Pechmann, and J.W. Gibbons. 1996. Structure and dynamics of an amphibian community: evidence from a sixteen-year study of a natural pond. Pp. 217-248 *In:* M.L. Cody and J. Smallwood (eds.). Long-term Studies of Vertebrate Communities. Academic Press, New York, NY

Semlitsch, R.D. and J.R. Bodie. 1998. Are small, isolated wetlands expendable? Conservation Biology 12: 1129-1133

Shirose, L.J and R.J. Brooks. 1997. Fluctuations in abundance and age structure in three species of frogs (Anura: Ranidae) in Algonquin Park, Canada, from 1985 to 1993. Herpetological Conservation 1: 16-26

Shirose, L.J., C.A. Bishop, D.M. Green, C.J. MacDonald, R.J. Brooks, and N.J. Helferty. 1997. Validation tests of an amphibian call count survey technique in Ontario, Canada. Herpetologica 53: 312-320

Sinsch, U. 1990. Migration and orientation in anuran amphibians. Ethology, Ecology, and Evolution 2: 65-79

Sjögren, P. 1991. Extinction and isolation gradients in metapopulations: the case of the pool frog (*Rana lessonae*) Biological Journal of the Linnean Society 42: 135-147

Sjögren-Gulve, P. 1994. Distribution and extinction patterns within a northern metapopulation of the pool frog, *Rana lessonae*. Ecology 75: 1357-1367

Skelly, D.K. 1995a. A behavioral tradeoff and its consequences for the distribution of *Pseudacris* treefrog larvae. Ecology 76 (1): 150-164

Skelly, D.K. 1995b. Competition and the distribution of spring peeper larvae. Oecologia 103: 203-207

Skelly, D.K., 1996. Pond drying, predators, and the distribution of *Pseudacris* tadpoles. Copeia 1996: 599-605

Skelly, D.K. 1997. Tadpole communities. American Scientist 85: 36-45

Skelly, D.K., E.E. Werner, and S.A. Cortwright. 1999. Long-term distributional dynamics of a Michigan amphibian assemblage. Ecology 80(7): 2326-2337

Skelly, D.K., L.K. Friedenburg, and J.M. Kiesecker. 2002. Forest canopy and the performance of larval amphibians. Ecology 83: 983-992

Smith, D.C. 1983. Factors controlling tadpole populations of the chorus frog (*Pseudacris triseriata*) on Isle Royale, Michigan. Ecology 64(3): 501-510

Smith, D.C. and J. Van Buskirk. 1995. Phenotypic design, plasticity, and ecological performance in two tadpole species. Am. Nat. 145: 211-233

Smith-Gill, S.J. and K. Berven. 1979. Predicting amphibian metamorphosis. Am. Nat. 113: 563-585

Snodgrass, J.W., M.J. Komoroski, A. L. Bryan, Jr., and J. Burger. 2000. Relationships among isolated wetland size, hydroperiod, and amphibian species richness: implications for wetland regulations. Conservation Biology 14: 414-419

Staniszewski, M.S. 1995. Amphibians in Captivity. T.F.H. Publications, Neptune, NJ, USA. 544 pp.

Stebbins, R.C. and N.W. Cohen. 1995. A Natural History of Amphibians. Princeton University Press, Princeton, NJ

Steinwascher, K. and J. Travis. 1983. Influence of food quality and quantity on early larval growth of two anurans. Copeia 1983: 238-242

Stevens, J. 1992. Applied multivariate statistics for the social sciences, 2nd edition. Lawrence Erlbaum, Princeton, NJ

Strijbosch, H. 1980. Habitat selection by amphibians during their terrestrial phase. British Journal of Herpetology 6: 93-98

Tejedo, M. and R. Reques. 1994. Does larval growth history determine timing of metamorphosis in anurans? A field experiment. Herpetologica 50: 113-118

Thomas, L. and K. Martin. 1996.The importance of analysis method for Breeding Bird Survey population trend estimates. Conservation Biology 10:479-490

Travis, J. 1994. Calibrating our expectations in studying amphibian populations. Herpetologica 50(1): 104-108

Trombulak, S.C. and C.A. Frissell. 2000. Review of the ecological effects of roads on terrestrial and aquatic communities. Conservation Biology 14: 18-30

Ultsch, G.R., D.F. Bradford, and J. Freda. 1999. Physiology: Coping with the environment. Pp. 189-214 *In* R.W. McDiarmid, R.A. Altig. (eds.) Tadpoles: The Biology of Anuran Larvae, Univ. Chicago Press, Chicago, IL

U.S. EPA. 2002. Methods for evaluating wetland condition: using amphibians in bioassessments of wetlands. Office of Water, U.S. Environmental Protection Agency, Washington, DC. EPA 822-R-02-022

Valderrama, J.C. 1981. The simultaneous analysis of total nitrogen and total phosphorus in natural waters. Mar. Chem. 10: 109-122.

van Buskirk, J. 2000. The costs of an inducible defense in anuran larvae. Ecology 81(10): 2813-2821

van Dorp, D. and P.F.M. Opdam. 1987. Effects of patch size, isolation, and regional abundance on forest bird communities. Landscape Ecology 1: 59-73

Varhegyi, G., S.M. Mavroidis, B.M. Walton, C.A. Conaway, and A.R. Gibson. 1998. Amphibian surveys in the Cuyahoga Valley National Recreation Area. Pp. 137-154 *in:* M. J. Lannoo, editor. Status and Conservation of Midwestern Amphibians. University of Iowa, Iowa City, Iowa, USA

Vogt, R.C. 1981. Natural History of Amphibians and Reptiles of Wisconsin. Milwaukee Public Museum, Milwaukee, WI

von Ende, C.N. 1993. Repeated-measures analysis: growth and other time-dependent measures. Pp. 113-137 *In:* S.M. Scheiner and J. Gurevitch (eds.). Design and Analysis of Ecological Experiments. Chapman and Hall, New York, NY

Vos, C.C. and J.P. Chardon. 1998. Effects of habitat fragmentation and road density on the distribution pattern or the moor frog, *Rana arvalis*. Journal of Applied Ecology 35: 44-56

Vos, C.C. and H.P. Stumpel. 1995. Comparison of habitat-isolation parameters in relation to fragmented distribution patterns in the tree frog (*Hyla arborea*). Landscape Ecology 11: 203-214

Waldick, R.C., B. Freedman, and R.J. Wassersug. 1999. The consequences for amphibians of the conversion of natural, mixed-species forests to conifer plantations in southern New Brunswick. The Canadian Field Naturalist 113: 408-418

Wassersug, R.J. and E.A. Seibert. 1975. Behavioral responses of amphibian larvae to variation in dissolved oxygen. Copeia 1975: 86-103

Watermolen, D.J. andH. Gilbertson. 1996. Keys for the identification of Wisconsin's larval amphibians. Wisconsin Endangered Resources Report #109, Bureau of Endangered Resources, Wisconsin Department of Natural Resources. Madison, WI

Weir, L. A. and M. J. Mossman. In press. The protocol and history of the amphibian calling survey of the North American Amphibian Monitoring Program (NAAMP). Chapter 39 *in:* M. J. Lannoo, editor. Declining amphibians: a United States' response to the global phenomenon. University of California, Berkeley, California, USA

Wellborn, G.A., D.K. Skelley, and E.E. Werner. 1996. Mechanisms creating community structure across a freshwater habitat gradient. Annual Review of Ecology and Systematics 27: 337-363

Weller, W.F. and D.M. Green. 1997. Checklist and current status of Canadian amphibians. Herpetological Conservation 1: 309-328

Welsh, H.W., Jr. 1990. Relictual amphibians and old-growth forests. Conservation Biology 4: 309-319

Welshmeyer, N.A. 1994. Fluorometric analysis of chlorophyll *a* in the presence of chlorophyll *b* and pheopigments. Limnol. Oceanogr. 39: 1985-1992

Werner, E.E. 1986. Amphibian metamorphosis: growth rate, predation rate, and optimal size at transformation. American Naturalist 128: 319-341

Werner, E.E. and K.S. Glennemeier. 1999. Influence of forest canopy cover on the breeding pond distributions of several amphibian species. Copeia 1999(1): 1-12

Wetzel, R.G. and G.E. Likens. 2000. Limnological analyses, 3rd ed. Springer-Verlag. 429 pp.

Wilbur, H.M. 1980. Complex life cycles. Annual Review of Ecology and Systematics 11:67-93

Wilbur, H.M. 1984. Complex life cycles and community organization in amphibians. *In:* P.W. Price, C.N. Slobodchikoff and W.S. Gaud (eds.). A New Ecology: Novel Approaches to Interactive Systems. John Wiley and Sons, New York, NY USA

Wilbur, H. M. 1987. Regulation of structure in complex systems: experimental temporary pond systems. Ecology 68: 1437-1452

Wilbur, H.M. and J.P. Collins. 1973. Ecological aspects of amphibian metamorphosis. Science 182: 1305-1314

Winter, T.C. 1988. Conceptual framework for assessment of cumulative impacts on the hydrology of non-tidal wetlands. Environmental Management 12: 605-620

Wyman, R.L. 1988. Soil acidity and moisture and the distribution of amphibians in five forests of south central New York. Copeia 1988: 394-399

Zar, J. R. 1998. Biostatistical Analysis. Fourth edition. Prentice Hall. Englewood Cliffs, New Jersey, USA

Zimmerman, B. L. 1994. Audio strip transects. Pages 92-97 *in:* W.R. Heyer, M.A. Donnelly, R.W. McDiarmid, L.C. Hayek, and M.S. Foster (eds). Measuring and monitoring biological diversity: standard methods for amphibians. Smithsonian Press. Washington, D.C., USA

Zug, G.R., L.J. Vitt, and and J.P Caldwell. 2001. Herpetology: an introductory biology of amphibians and reptiles (2nd ed.). Academic Press.